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Species Richness, Diversity, and Abundance of Sponge Communities in Broward County, Florida, 2000-2015

Jessica Price
Nova Southeastern University, jessica.price55@gmail.com

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Jessica Price

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Approved:
Thesis Committee

Major Professor: Charles Messing, Ph.D.

Committee Member: David Gilliam, Ph.D.

Committee Member: Jose Lopez, Ph.D.

HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

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By

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Abstract

Sponges (Porifera) are a major component of coral reef ecosystems. They outnumber coral species on the Florida Reef Tract, and in places, account for more living cover. Because coral reefs are a vital part of Florida's economy, it is important to understand how local sponge assemblages vary spatially and temporally, especially as corals continue to decline. However, long-term observations of sponge assemblages (species richness, diversity and abundance) are lacking. To address this, annual photoquadrats were analyzed from a series of 25 sites off Broward County between 2000 and 2015. Variations in sponge assemblages were then compared to several natural and anthropogenic stressors. Statistical analysis via PERMANOVA, PERMDISP and linear mixed-effect *(lme)* models revealed significant changes in total sponge composition, with spatial and temporal trends evident among different habitat types and sites. A total of 85 species were identified to the lowest taxonomic level. Common species included *Spirastrella coccinea*, *Niphates erecta*, *Aplysina cauliformis*, and *Amphimedon compressa.* Species richness increased with depth and habitat type. The Linear Middle Reef had the highest species abundance and richness, while the Shallow Ridge had the lowest of both. Contrary to trends seen in coral species, sponge composition did not decrease with an increase in latitude. Natural fluctuations in sponge abundance and richness via the sponge loop were intensified by natural events. Five common species (*Amphimedon compressa*, *Aiolochroia crassa*, *Desmapsamma anchorata*, *Ircinia strobilina*, and *Xestospongia muta*) were selected to monitor growth and mortality over time. All species except for *Am. compressa* had significant change in area from 2000 to 2015, and *D. anchorata* exhibited faster growth rates than all other species. This 15-year study provides a baseline of sponge assemblages on the Southeast Florida Reef Tract and insights into individual sponge communities. Sponges are essential organisms on coral reefs. As hard coral continues to decline, and natural and anthropogenic events intensify, this baseline data will serve to inform future studies.

Keywords: SEFT, Sponge, Broward County, RC, CPS, LIR, LMR, LOR

1. Introduction

Despite only covering a small percent of the world's ocean, coral reef systems are biologically and economically important (Carpenter *et al.*, 2008). These ecosystems are estimated to contain between one and ten million species, with fewer than ten percent identified (Small *et al.*, 1998; Spalding, 2001; Bouchet, 2006; Plaisance *et al.*, 2011), and they are critical to fisheries worldwide, especially along coasts (Cesar *et al.*, 2003; Stocker *et al.*, 2013). However, the continuous decline of reef systems over the last several decades due to climate change and local environmental factors has become a major concern (Hughes, 1994; Hughes *et al.*, 2003; Wilkinson, 2008; Burke *et al.*, 2011; Stocker *et al.*, 2013). These influences have shifted species dominance on coral reefs from hard corals to soft corals and algae, and may negatively affect businesses reliant on reef biodiversity (Hoegh-Guldberg *et al.*, 2007; Mumby and Steneck, 2008; Burke *et al.*, 2011; Stocker *et al.*, 2013; Maynard *et al.*, 2017; Bartlett *et al.*, 2018).

Sponges (phylum Porifera, chiefly class Demospongiae) are important components of coral reef systems worldwide. In South Florida and elsewhere, they are abundant, diverse (Rützler and I.G., 1982; Jaap, 1984; Dodge *et al.*, 1989; 1991b; Diaz and Rutzler, 2001; Gilliam, 2012), and may outnumber corals and cover a greater percent of local reef and live bottom substrates. For example, a Broward County beach renourishment study recorded ~50 to >150 sponges belonging to ~40 species but only 4-29 coral colonies belonging to 15 species per 4-m^2 quadrat (Dodge et al., 1991). The decline of stony corals along the Southeast Florida Reef Tract offers the possibility that sponge populations and relative dominance may increase over time (McMurray *et al.*, 2010). In addition, increased ocean temperatures and acidification do not appear to have significant effect on sponge populations (Carballo *et al.*, 2008; Bell *et al.*, 2013; Halperin, 2014). Since coral reefs are a vital part of Florida's economy, it is important to understand the population dynamics of sponges.

This study examines the composition, richness, diversity, and abundance of sponge assemblages along a series of 25 transect sites in Broward County, Florida, over a 15-year period. Sponges were identified, and counted, and areas of selected species examined in

0.75-m^2-photoquadrats to investigate changes in assemblages (species richness, diversity, and abundance) relative to habitat over time. Climate data and local development reports revealed that at least some changes can be linked to natural and anthropogenic events (OAI, 2011). Growth and mortality rates of five morphologically distinct common species were also calculated to examine how growth type may contribute to longevity of sponges. Knowledge of changes in sponge composition in southeastern Florida over time will assist in understanding the functional roles of sponge communities on local reefs and how those roles have changed or may change in the future if hard coral populations continue to decline.

1.1 Ecological Importance

Sponges are simple sessile metazoans with an aquiferous system consisting of external pores leading to and from an internal interconnected series of canals and flagellated chambers (Hooper *et al.*, 2002). The skeleton is composed of siliceous or calcareous elements called spicules, and/or spongin fibers composed of collagen (Van Soest *et al.*, 2012). Specialized cells called choanocytes bear a flagellum that generates the feeding and respiratory current through the body, and a ring of micovilli captures suspended food particles (Hooper *et al.*, 2002; Bell *et al.*, 2017a). Sizes range from one centimeter to several meters across (Wulff, 2006). Growth forms span a wide range and include encrusting, branching, spherical, columnar, and massive (Hooper *et al.*, 2002; Humann, 2002; Zea *et al.*, 2014). However, both growth form and color are frequently highly plastic, often making identification difficult (Van Soest *et al.*, 2012). Small specimens may be particularly difficult to identify. Sponges are excluded from many long-term coral reef monitoring projects, because many are difficult to identify; they may occupy less cover than corals (Bell, 2008), and they are generally not thought to have the same importance as corals on reef ecosystems. In addition, their growth rates are indeterminate and cannot be measured by annual growth rings, and they often suffer from high partial mortality (Wulff, 2008).

Recent instabilities in reef composition have resulted in shifts of species dominance (Hughes, 1994; Maliao *et al.*, 2008). As one of the dominant groups of organisms on local reefs, sponges may play a large role these ecosystem changes (Wulff, 2006; Carballo *et al.*, 2008; Gilliam, 2012; Pawlik *et al.*, 2018). Although sponges are not traditional reef builders, certain species contribute to the framework of reefs due to interactions with other organisms (Maldonado *et al.*, 2015). Members of the encrusting family Clionaidae often overgrows boulder corals such as *Montastraea cavernosa* and act as major reef bioeroders (Holmes, 1997; Carballo *et al.*, 2013; Halperin, 2014). Several branching species attach to corals as a means of anchoring and compete with corals for space (Wulff, 2008; Meurer *et al.*, 2010; Mclean *et al.*, 2015).

As filter feeders, sponges play an important role in coral reef food webs. On a productive reef, they are able to filter the equivalent of the entire water column in one day (Reiswig, 1974; Pawlik *et al.*, 2018). Sponges absorb enormous amounts of dissolved organic matter in addition to particles, and release the equivalent of up to 40% of it as particulate organic carbon (McMurray *et al.*, 2018). Many invertebrates and vertebrates feed not only on the sponges but also the particulate organic matter released as their metabolic waste (de Goeij *et al.*, 2013; Maldonado *et al.*, 2015). Fishes and invertebrates such as polychaetes and shrimp often use the canal system of sponges as habitat (Van Soest *et al.*, 2012). Apart from other possible factors such as substrate availability and fresh-water outflows, reef sponge diversity appears to depend on depth; at depths less than 10 m sponges are smaller and species richness is lower (Bell, 2007; De Voogd and Cleary, 2008).

As in other coastal regions, Florida's reefs have been in decline since the 1980s, with losses in hard coral cover and increasing dominance of soft coral and macroalgae (Lessios, 1988; Precht and Miller, 2007). However, sponges appear to have been less affected by these changes (Freeman *et al.*, 2007; Maliao *et al.*, 2008). Engel (2005) estimated that Southeastern Florida has as many as 60 reef-associated sponge species, and Klaus Rützler (Smithsonian Institution, personal communication to CG Messing) estimated that the tropical western Atlantic supports several hundred shallow-water species. Different local studies have recorded different numbers, e.g., 34 (Peddycoart, 2010) and 55 (Dodge *et al.*, 1989)off Broward County, and 43 off Key Largo (Engel and Pawlik, 2005). Sathe (2008) observed that sponge density varied with reef habitat, and ranged from 30/m^2 on the Linear Middle Reef to 2.97/m^2 on the Shallow Inshore Ridge. (Bush, 2012) followed post-injury recovery, survival and growth of the giant barrel sponge, *Xestospongia muta*, over a 15-month period. Common local species include *Amphimedon compressa, Callyspongia vaginalis, Desmapsamma anchorata, Iotrochota birotulata, Ircinia felix, Niphates erecta, Spirastrella coccinea,* and *Scopalina ruetzleri,* (Dodge *et al.*, 1989; Thanner, 2004; Peddycoart, 2010).

1.2 Southeast Florida Coral Reef Tract (SEFRT)

The northern part of the Southeast Florida Coral Reef Tract extends 125 km from West Palm Beach to South Miami (Banks *et al.*, 2008). The tract exhibits a variety of` habitats, including a series of linear reefs and ridge complexes (Walker *et al.*, 2008). Depth and bottom type, as described by Banks *et al.* (2008) and Walker (2012), characterize each:

The Nearshore Ridge Complex (NRC): depth 3-5 m; shallow ridges **(RC)** and colonized pavement **(CPS)** of flat, low relief solid carbonate rock with highly variable coverage.

Inner Reef (LIR): depth ~8 m; coral-rich reef dominated by immature reef formations and crests.

Middle Reef (LMR): depth ~15 m; relatively continuous coral reef supporting a diverse community.

Outer Reef (LOR): depth ~16 m; relatively continuous shore-parallel reef including back reef, reef crest, and spur and groove habitats.

Located within 3 km of an urbanized coast, the SEFRT is affected by anthropogenic and natural stressors (Dodge *et al.*, 1989; Sathe, 2008; Halperin, 2014). Pollution from this heavily populated area includes nutrient runoff and sewage outflow. Port Everglades, Boca Inlet, and Hillsboro Inlet are major sources of freshwater that transport runoff from intra-coastal waterways into the Atlantic Ocean (Campbell *et al.*, 2015).

Tourism plays a key role in Florida's economy. The annual contribution from this industry averages ~6 billion U.S. dollars each year, but it often has a negative effect on coral reefs (2018). Ship groundings, dropped anchors, and scuba divers/snorkelers make contact with the reef, and lost fishing gear can destroy parts of the reef (Florida Department of Environmental Protection, 2016) . In addition, as tourism and the local population have increased, so have commercial/coastal development and the need to replenish local beaches, which has resulted in coastal dredging and attendant suspended sediments (2018). Recent beach renourishments have included Hollywood Beach, Dania Beach, and John Lloyd State Park in 2005 and 2006, Deerfield Beach and Hillsboro Inlet in 2011, Hollywood Beach in 2012, and John Lloyd State Park again in 2013 (2018). Note that, although John U. Lloyd State Park (JUL) was renamed in 2016 as Dr. Von D. Mizell-Eula Johnson State Park, this paper uses the JUL designation current when the photographs were taken.

Broward County, like many other tropical coastal counties, often deals with tropical storms and hurricanes, and Florida is more likely to be hit by a tropical storm or hurricane than any other state in the United States (Malmstadt *et al.*, 2009). These storms tend to occur between 1 June and 30 November due to the mixing of warm ocean temperatures and rapidly cooling atmospheric temperatures (NOAA, 2016). Hurricanes not only have the potential to affect coastal cities but can also affect coral reefs, causing mortality to reef organisms via powerful wave action, currents, and suspended sediment. In the last twenty years, southeastern Florida has experienced seven tropical storms and six hurricanes (NOAA, 2016).

1.3 Research Goals

Although sponges often outnumber coral colonies in abundance and diversity, no long-term monitoring projects along the SEFRT have considered them in detail (Diaz and Rutzler, 2001). As previously mentioned, several short-term monitoring projects provided a baseline of species present. Thanner (2004) monitored sponges and other benthos on artificial modules over an 8-year period, and Peddycoart (2010) examined them on natural reefs between 2002 and 2006. However, a long-term project would establish not only what sponge species are present, but how assemblages change over time, increasing the understanding of local sponge community dynamics.

Due to the high plasticity of sponge morphology and the great number of often difficult to identify species, few investigations have focused on processes such as recruitment, growth, and mortality in reef sponges. Several studies suggest massive growth forms and small encrusting species live longer than branching and rope/runner species, especially in high-energy environments (Bell and Barnes, 2003 ; Wulff, 2008). However, larger species allocate more resources to protection over quick growth (Pawlik *et al.*, 2008; Loh and Pawlik, 2014). To address this deficiency, this project examined growth and mortality in five common species with substantially different growth forms: brightly colored massive *Aiolochroia crassa*, red rope/runner *Amphimedon compressa*, weedy and encrusting *Desmapsamma anchorata*, massive, ball-shaped *Ircinia strobilina*, and massive, barreled-shaped *Xestospongia muta*.

1.4 Hypotheses

1) Sponge assemblage composition (species richness, diversity, and abundance) relative to habitat changed over time and can be linked to natural (significant variation in sea temperature and impacts from storms) and anthropogenic events (dredging and renourishment).

2) Change in sponge growth/mortality over time differed significantly among species; e.g., growth rate of *Desmapsamma anchorata* is more rapid than the moderate rate of *Amphimedon compressa* and slow-growing *Xestospongia muta* (Wulff, 2008; Mercado and Yoshioka, 2009; McMurray *et al.*, 2010; Bush, 2012).

2. Materials and Methods

2.1 Monitoring Sites

Beginning in 2000, Nova Southeastern University (NSU) took over a project monitoring the entire reef tract along Broward County. The Broward County Commission began the project in 1997 with 18 sites; five sites were added in 2000, and two more in 2003 for a total of 25 (Figure 1). The sites span about 49 km of SEFRT (Figure 2), beginning just north of Boca Inlet (BOCA1) and ending just south of Hollywood Beach

(HH). Up to three sites are arranged in roughly east-west lines off coastal cities to insure coverage of inshore-to-offshore variations in reef environments. As a result, depth, substrate and habitat vary among sites (Table 1).

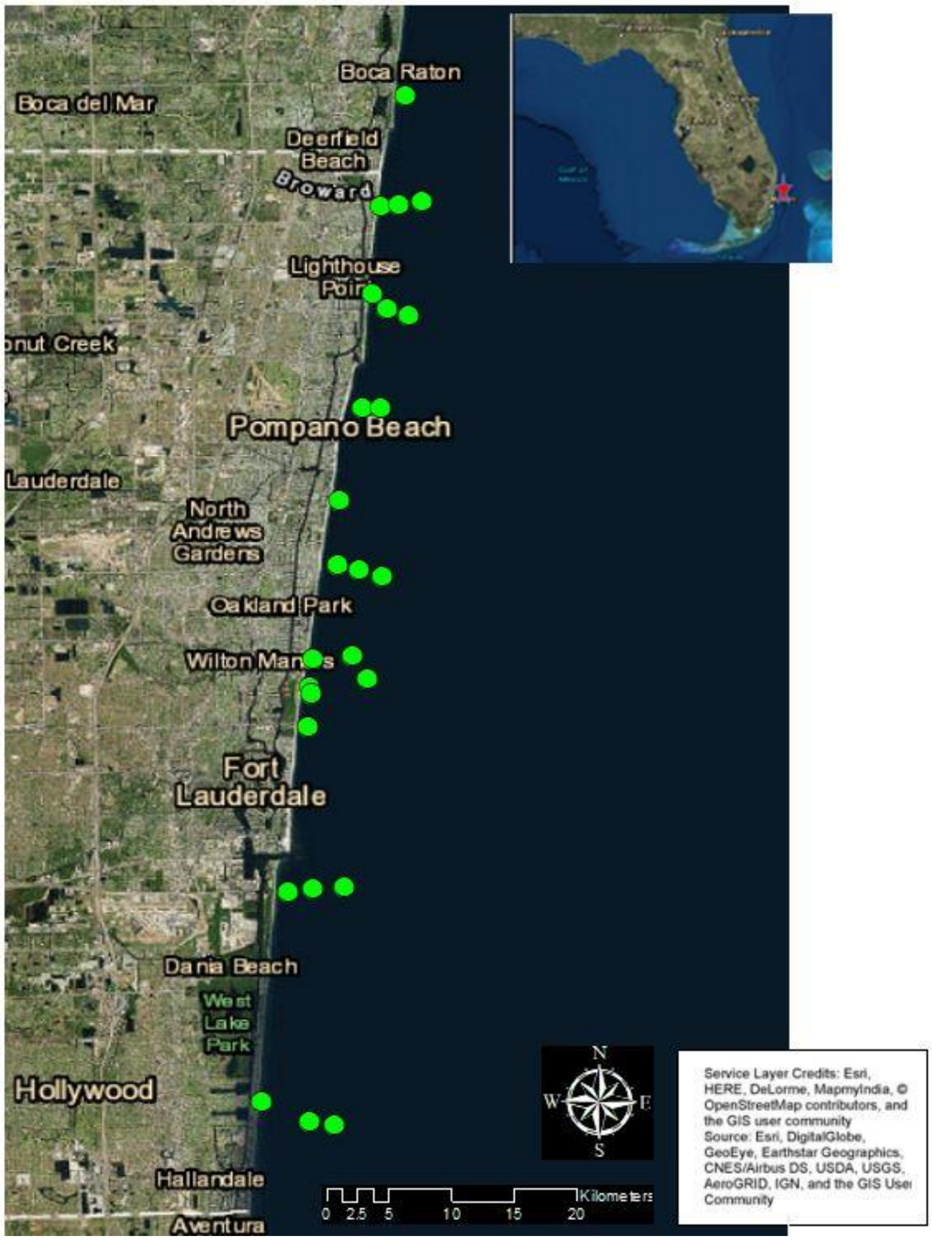


Figure 1: Site locations, adjacent to Broward County cities.

Table 1: Depth and habitat type by site. Site names are abbreviated for the adjacent beach: BOCA= Boca Raton, DB= Deerfield Beach, FTL= Fort Lauderdale, HB= Hillsboro Beach, HH= Hollywood Beach, JUL= John Lloyd State Park, POMP= Pompano Beach.

Site Name	**Habitat type**	**Depth (m)**
JUL6	Ridge-Shallow	3.66
DB1	Ridge-Shallow	5.49
POMP1	Ridge-Shallow	6.1
POMP4	Ridge-Shallow	6.1
HH2	Colonized Pavement-Shallow	5.79
FTL1	Colonized Pavement-Shallow	5.79
FTL4	Colonized Pavement-Shallow	6.1
FTL5	Colonized Pavement-Shallow	7.62
FTL6	Colonized Pavement-Shallow	7.62
HB1	Colonized Pavement-Shallow	6.4
POMP5	Colonized Pavement-Shallow	9.45
JUL7	Linear Inner Reef	9.75
JUL1	Linear Middle Reef	12.19
FTL2	Linear Middle Reef	14.63
POMP2	Linear Middle Reef	14.63
HB2	Linear Middle Reef	10.67
DB2	Linear Middle Reef	11.28
BOCA1	Linear Middle Reef	9.14
POMP6	Linear Middle Reef	15.58
JUL2	Linear Outer Reef	15.58
JUL8	Linear Outer Reef	15.24
FTL3	Linear Outer Reef	18.29
POMP3	Linear Outer Reef	15.54
HB3	Linear Outer Reef	14.94
DB3	Linear Outer Reef	16.76

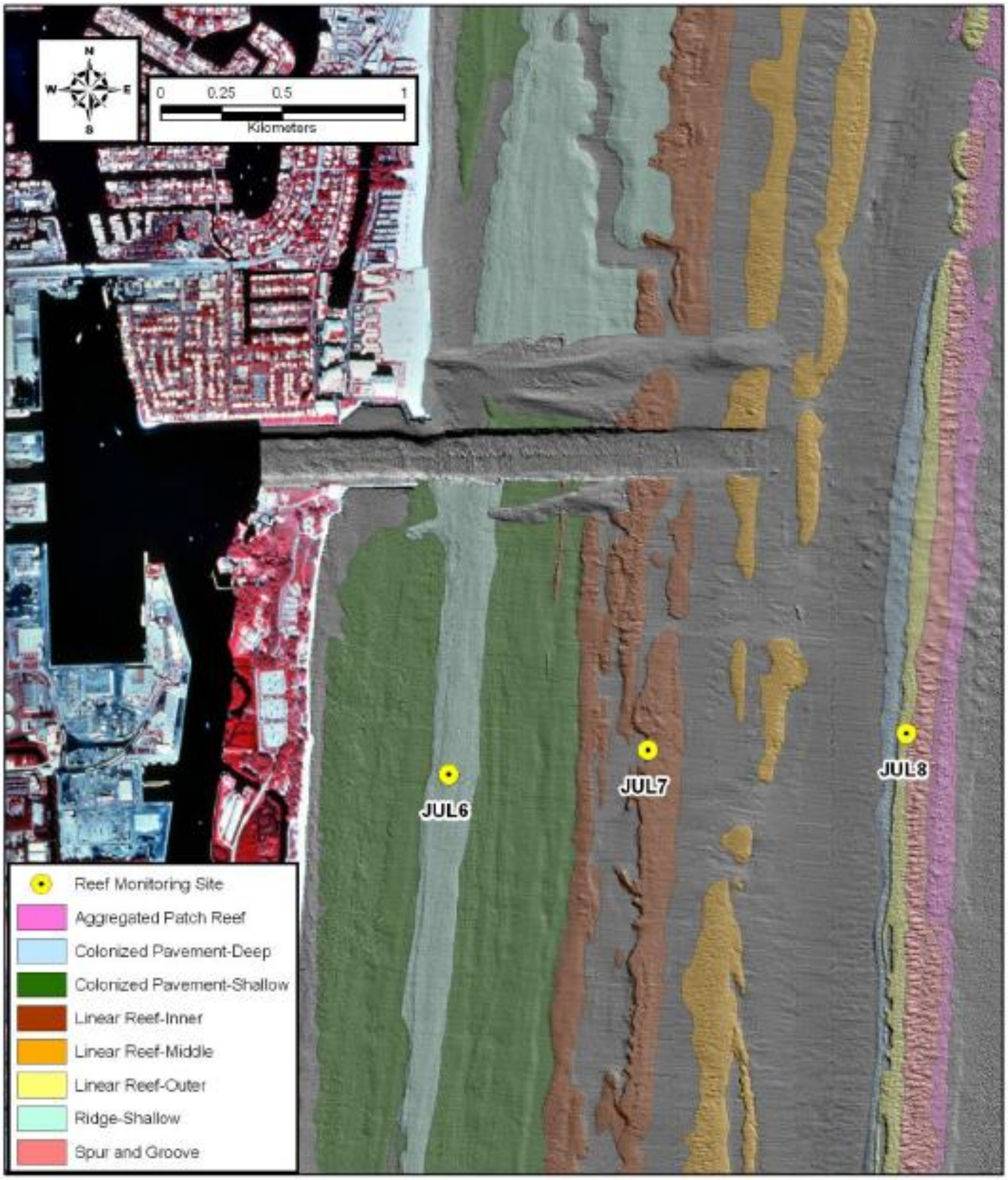


Figure 2: An example of a site location, JUL (John Lloyd State Park), and reef type using laser airborne depth sounder (LADS) bathymetry data (Walker et al., 2008).

2.2 Transects and Photoquadrats

Each site consisted of a 20-m-long transect oriented roughly north-south and established by permanent steel pins placed at 1-m intervals to ensure that the same substrate would be imaged by scuba divers in each annual monitoring effort. Photographs were taken in 2000-2001 using a Nikanoos underwater camera and slide images were then scanned into computer. From 2000-2015 images were captured using various digital cameras attached to a 0.75/m^2 (1.0 x 0.75 m) PVC quadrat frame to ensure the same area of seafloor was covered in each image. Each transect consisted of a series of 40 photoquadrats. A scuba diver would swim along the transect line beginning on the left side of the northernmost pin, placing the frame lengthwise so that 20 images would be taken. Then, reversing direction, the diver would capture 20 more images along the right side of the transect line, ending on the right side of the northernmost pin (Sathe, 2008; Peddycoart, 2010) (Figure 3). Images of each transect thus covered 30/m^2 of seafloor (40 x 0.75 m^2). Image identifiers for site and quadrat number were placed in the top right corner of each framer, while year and month were in the top left corner (Figure 4).

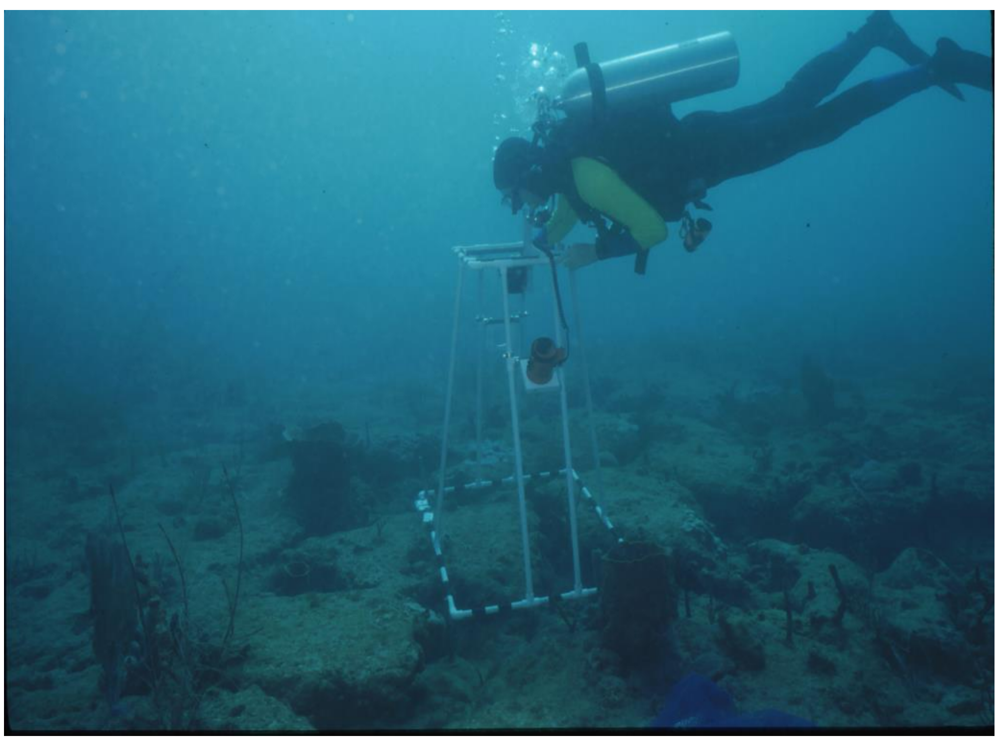


Figure 3: Diver taking a photo of a quadrat.

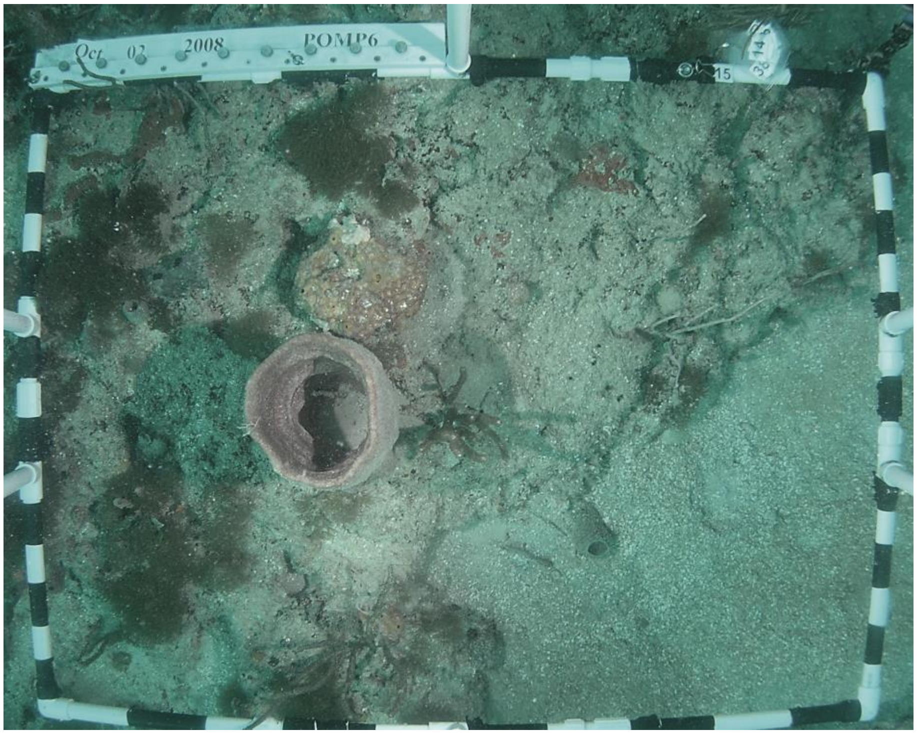


Figure 4: Example of a photoquadrat. Note the date in the top left corner and quadrat number in the upper right corner.

Because technology and management efforts improved after NSU assumed monitoring responsibilities, only photos from 2000 to 2015 were assessed. No images were taken during 2009, as no funding was available. After an initial examination of all images taken during the first two years (2000 and 2001), species composition of every fourth photo, with the addition of photoquadrat one, was compared to the total composition of each year using t-tests to determine whether the overall composition of sponge assemblages at each site could be accurately captured without examining every image in each transect. Since p-values were >0.05 for all sites, the same 11 of 40 photoqaudrats from each site were analyzed each year (Figure 5).

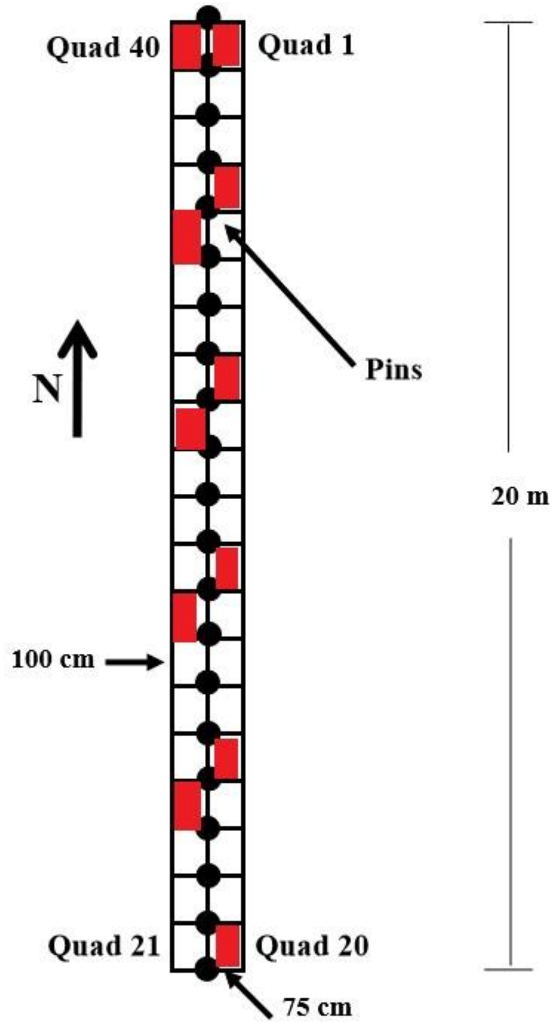


Figure 5: Example of transect site. Note red boxes represent 11 photoquadrats used from 2000 to 2015.

2.3 Coral Point Count with Excel extensions (CPCe)

To address the second hypothesis, images of five common species were selected to examine growth and mortality across a variety of morphotypes. The original 40 photoquadrats were browsed for the first several years, and photoquadrats were chosen at each site based on clarity of the selected species within the image. As a result, data was not collected uniformly at all sites, as selected species were not uniformly prevalent at all sites. Each selected image was uploaded to Coral Point Count with Excel extensions software

(CPCe) (Kohler, 2006) to measure growth of each individual sponge within the photoquadrats over the duration of the study and identify instances of partial or complete mortality. A *Bamboo* pen mouse was used to measure areal coverage of each species in each image (Figure 6). One hundred eight photoquadrats were analyzed among 23 sites.

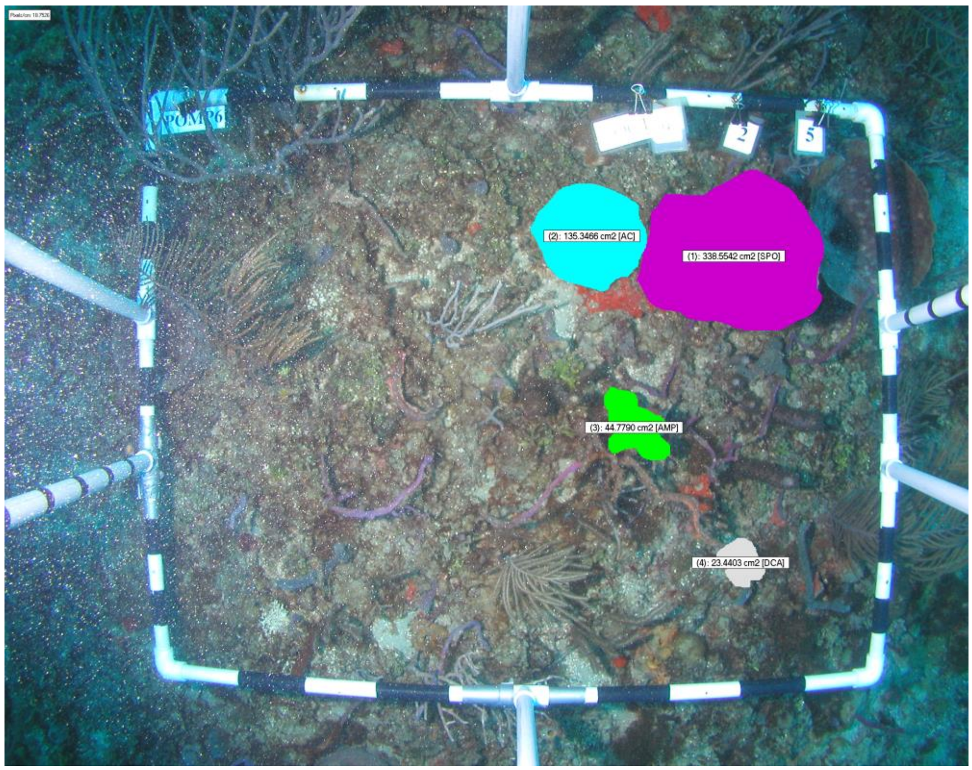


Figure 6: Example of CPCe sponge area outlines.

Table 2: Total number of individuals of each species measured at each site.

Site	*Am. compressa*	*Ai. crassa*	*D. anchorata*	*I. strobalina*	*X. muta*
BOCA1	36	2	18	6	1
DB1	1	0	0	0	0
DB2	14	6	26	5	3
DB3	4	7	0	0	8
FTL1	3	0	0	0	0
FTL2	28	5	0	6	6
FTL3	6	2	0	1	4
FTL4	14	0	0	4	1
FTL5	4	0	0	3	0
FLT6	0	0	14	1	0
HB1	0	0	2	4	0
HB2	7	0	3	3	5
HB3	19	14	0	2	6
JUL1	14	3	0	3	2
JUL2	24	5	5	8	13
JUL6	4	0	0	0	0
JUL7	12	0	2	2	5
JUL8	6	7	0	5	1
POMP1	1	0	0	1	0
POMP2	8	7	0	2	3
POMP3	20	8	6	7	4
POMP4	2	0	0	3	0
POMP5	9	0	0	3	0
POMP6	17	9	9	4	5
Total	**253**	**75**	**85**	**73**	**67**

2.4 Statistical Analysis.

Statistical analyses were carried out on 4,026 images. Because no thorough taxonomic picture keys are available for southeastern Florida sponges, all identifications were made using "The Sponge Guide, a picture guide to Caribbean sponges" (http://spongeguide.org) and The Interactive Sponge Guide of south Florida Sponges" (https://guide.poriferatreeoflife.org). Sponges that could not be identified to species in photographs were labeled as unknown species alphabetically, e.g., unknown brown species A, and differentiated by color and morphology. To address the hypotheses, all tests were performed using “Biostatistical Design and Analysis Using R” and the Plymouth Routines In Multivariate Ecological Research (PRIMER) (Murray, 2010; Clarke and Warwick, 2014).

2.4.1 Total Sponge Composition

Simpson’s diversity index, Shannon-Wiener diversity index (Equations 1, 2), and Pielou’s evenness measurements (Equation 3) were calculated for each site and compared among years to determine assemblage structure (DeJong, 1975; Dodge *et al.*, 1991b).

Shannon-Wiener Index

(Equation 1) $$H' = -\sum_{i=1}^{S} P_i \log_2 P_i$$

Simpson’s Diversity Index

(Equation 2) $$1 - \sum_{i=1}^{k} \frac{n_{i(n_i-1)}}{n(n-1)}$$

Pielou’s Evenness Measurement

(Equation 3) $$J' = \frac{H'}{H'max}$$

Matrices of Bray-Curtis Similarity coefficients were generated from species diversity and abundance. From these coefficients, plots were created using non-metric multi-dimensional scaling (nMDS), which provides a visual representation of community composition across reef types (Kruskal and Wish, 1978; Thanner, 2004; Sathe, 2008; Somerfield *et al.*, 2008). Because the data distribution was uneven, sponge abundance and richness among sites was tested using a non-parametric three-factor permutational multivariate analysis of variance (PERMANOVA), which can analyze complex datasets (Anderson and Santana - Garcon, 2015). The PERMANOVA was designed with year as a fixed factor with 15 levels (for 2000 to 2015 minus 2009), reef as a fixed factor with 5 levels, and site as a random factor with 25 levels nested within reef (Somerfield *et al.*, 2008; Powell *et al.*, 2014).

A test for homogeneity of multivariate dispersions (PERMDISP) analysis was used as a pairwise comparison of dispersion to determine which sites and years from the PERMANOVA results had significance (Anderson and Santana, 2015). The timing of notable natural and anthropogenic events was then examined relative to sites to identify possible corresponding variations in sponge assemblages, composition and abundances. In addition, the average composition of each site over the 15 years was used to compare sites by depth category and reef type.

2.4.2 Growth and Mortality of Five Common Sponge Species

Linear Mixed-Effects Models (*lme*) (Laird and Ware, 1982) from the *nlme* package (Pinheiro *et al.*, 2014) in R Studio were used on each species to investigate species-specific growth and mortality over time, with area as the response variable and year as the fixed factor. Site was used as a random factor and nested within year. To reduce the number of factors, area was summed at each site by year. For all models with significance, a *Tukey's post-hoc* analysis was performed using the general linear hypothesis (*glht*) (Bretz *et al.*, 2016) function in the multcomp package (Hothorn *et al.*, 2017). For a pairwise comparison of years, a *Tukey's post-hoc* analysis was run to determine which combination of years had the greatest effect on *lme* significance. Log transformed scatterplots using the *ggplot* package (Wickham, 2016) were created to show area visually over time.

3. Results

3.1 Hypothesis One

3.1.1 Total Sponge Composition

Over the 15-year sampling period, 18,241 sponges were identified to lowest practical taxonomic level within the 11 photoquadrats at each site. Identified taxa belonged to 85 species in 36 genera, 27 families, and 16 orders. Twenty-five of the sponges could not be identified to species and were labeled as such, e.g., unknown brown species A or unknown pink encrusting species A. Aplysinidae was the most common family (10 species), followed by Niphatidae (6), and Agelasidae, Clionaidae, Irciniidae, each with four species (Figure 7). *Spirastrella coccinea* was the most common species and was present at every site. S*pirastrella. coccinea* accounted for 13% of total abundance, averaging 499 y^{-}

[1] individuals a year (Figure 8). Other common species included *Niphates erecta* (352 y^{-1} at 21 sites), *Amphimedon compressa* (343 y^{-1}at 19 sites) and *Aplysina cauliformis* (238 y^{-1} at 17 sites) (Figure 8). Due to their abundance in all habitats, they were not the focus of analyses of species composition by reef type.

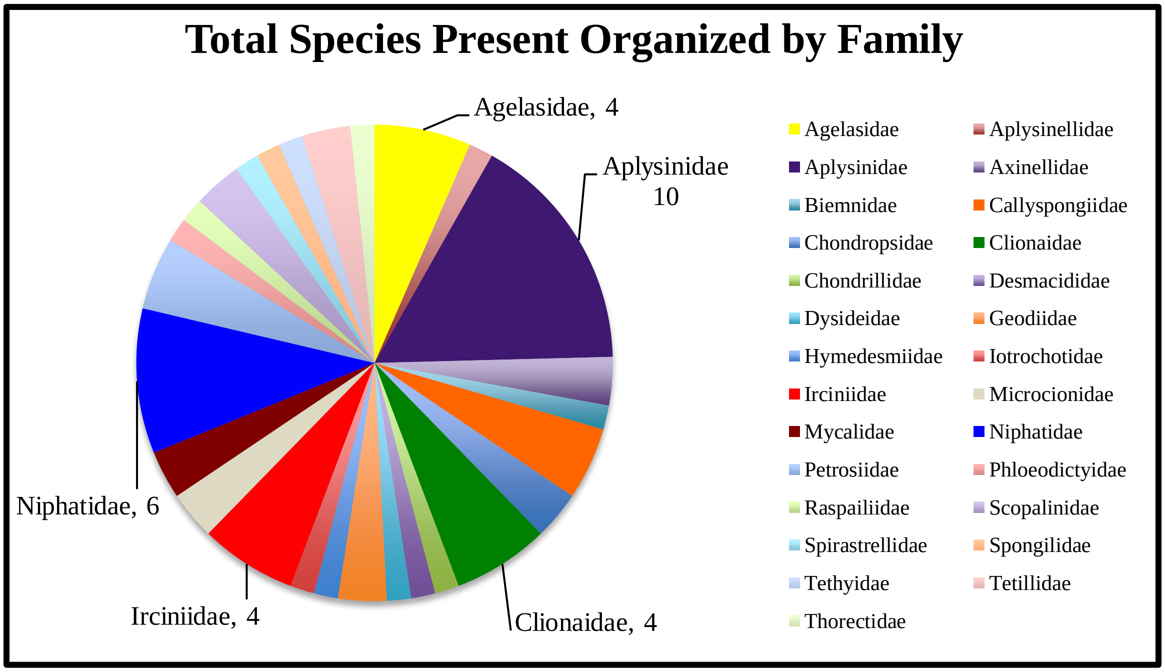


Figure 7: Total number of each species organized by family. Note common families: Aplysinidae (purple), Niphatidae (blue), Agelasidae (yellow), Clionaidae (green) and Iriciniidae (red).

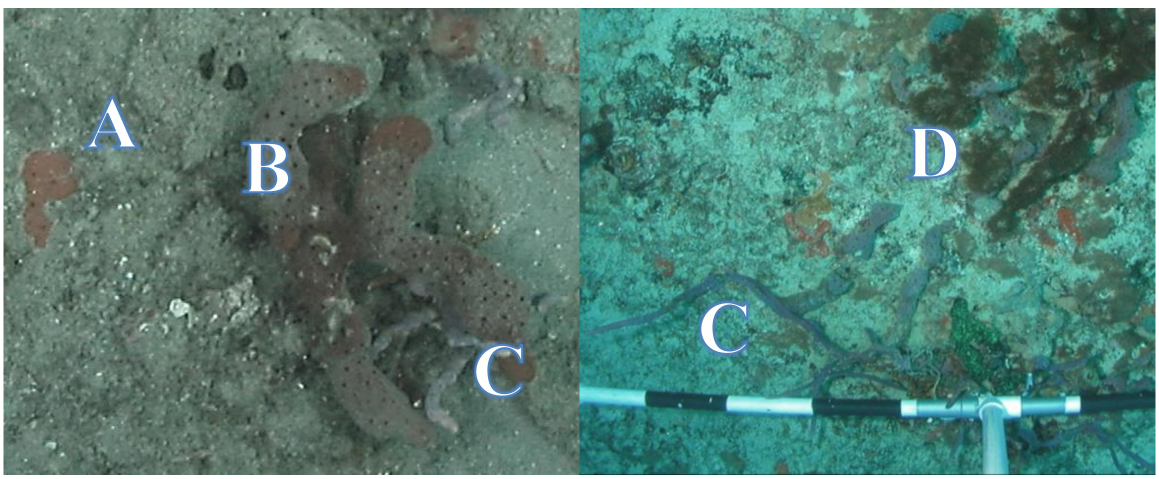


Figure 8: Photos of the most common species: 1. ***A:*** Spirastrella coccinea, ***B:*** Amphimedon compressa. *2.* ***C:*** Aplysinia cauliformis, ***D:*** Niphates erecta.

The maximum number of species present in a single year was 62 in 2004 (Figure 10). Pielou's Evenness Measurement (J' - 0.698606) remained constant throughout, and the diversity indices, Shannon-Weiner (H' - 2.831762) and Simpson's (1-lambda' - 0.90348) indicated a constant relatively high species diversity from year to year (Table 3). However, different reef habitats and individual sites showed greater variation (Figure 9). Linear Middle Reef (LMR) had the greatest number of species (46) and highest abundance (1147). Individual sites HB3 (27) and BOCA 1 (25) had the greatest species richness within a single year. Linear Outer Reef (LOR) sites HB3 (248) and POMP3 (233) had the highest abundance within a single year.

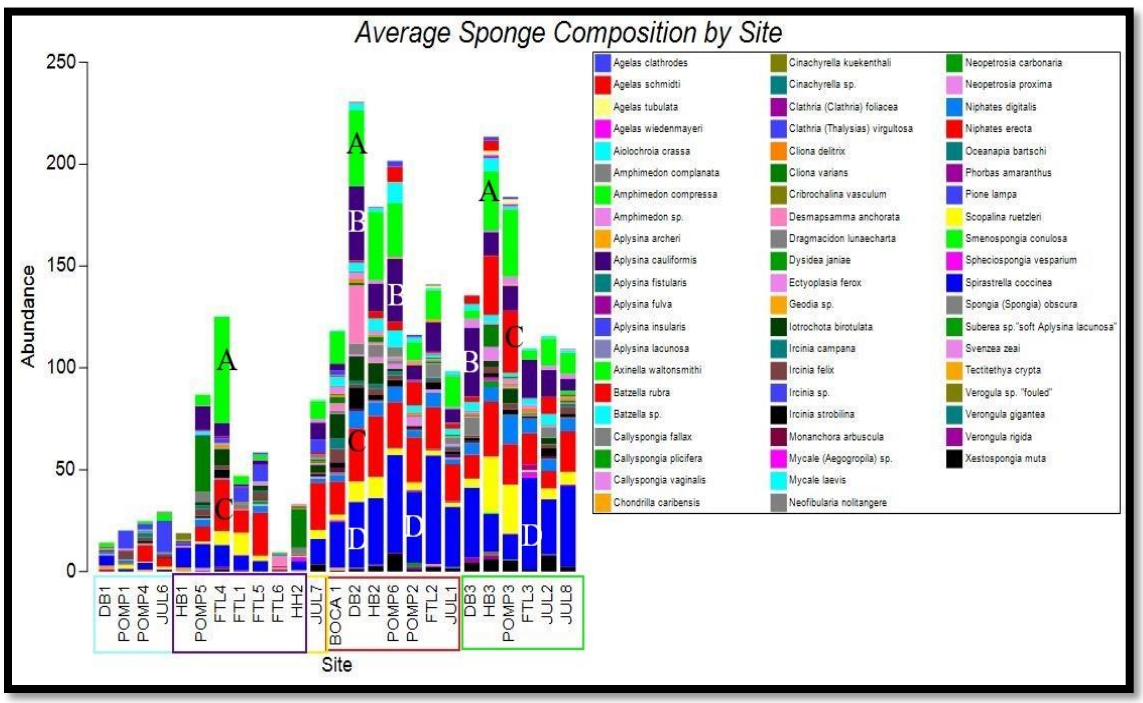


Figure 9: Stacked bar plot of the average species composition at each site (excluding unknown species). Sites are listed north to south by reef type; RC (blue), CPS (purple), LIR (yellow), LMR (red), LOR (green). Note common species indicated by letters: ***A:*** Amphimedon compressa *(lime green),* ***B****:* Aplysina cauliformis *(purple),* ***C****:* Niphates erecta *(red) and* ***D:*** Spirastrella coccinea *(blue).*

Table 3: Total richness(s), Abundance (N), Evenness (J'), Shannon-Weiner Index (H') and Simpson's Diversity Index (1-Lambda')2000-2015 across all sites.

Year	S	N	J'	H'(loge)	1-Lambda'
2000	53	2130	0.732422	2.907929	0.916518
2001	58	2083	0.712762	2.894131	0.914278
2002	57	2460	0.697827	2.821352	0.902008
2003	58	2864	0.676883	2.748446	0.888166
2004	62	2645	0.672649	2.776113	0.891601
2005	59	2526	0.697512	2.844133	0.897496
2006	58	2337	0.702461	2.852302	0.904414
2007	59	2646	0.692898	2.825319	0.902431
2008	60	2598	0.697638	2.85637	0.904739
2010	59	2459	0.695595	2.836314	0.905701
2011	58	2516	0.697261	2.831187	0.903742
2012	57	2468	0.693226	2.802748	0.901838
2013	55	2690	0.710554	2.847428	0.906783
2014	55	2564	0.705102	2.82558	0.907444
2015	57	2681	0.694297	2.807079	0.905036

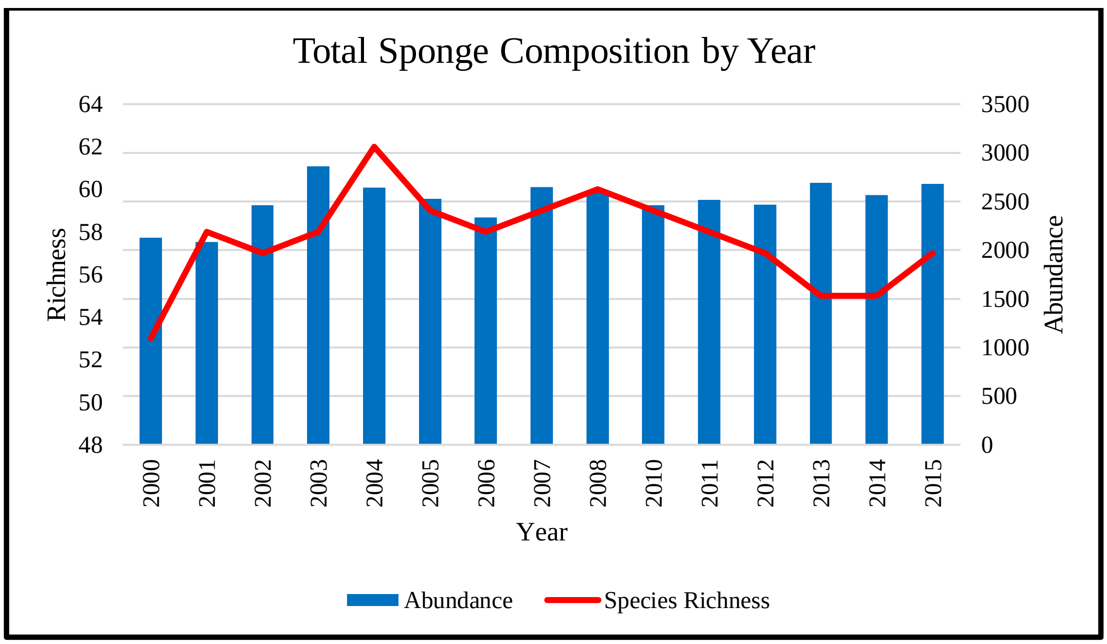


Figure 10: Total species richness and abundance at all 25 sites by year. Richness ranged from 53 in 2000 to 62 in 2004. Abundance ranged from 2083 in 2001 to 2864 in 2003.

3.1.2 Multivariate analysis

The nMDS plot created from the Bray-Curtis similarity index shows a distinct separation in sponge communities between the shallow ridge (RC) (blue) and the other habitat types (Figure 11). The closer the points are to each other, the higher the similarity in average sponge composition. The Inner (LIR), Middle (LMR) and Outer (LOR) Linear Reefs share a 60% similarity of sponge composition with several of the colonized pavement sites (CPS). Although these reefs are not definitely separated, certain sites differ significantly by depth (Figure 12). This pattern is explored below with the PERMANOVA and multiple PERMDISP.

Results of the three-way PERMANOVA indicate significant change in sponge composition between years, reef types, and the sites nested within each reef (Table 4). The Pseudo-F statistic (417.35) suggests a dispersion effect and that most of the significant change is between the different reef types. PERMDISP of year, reef type, and site were compared to investigate any dispersion effect. For instance, there was significant change in total sponge composition from 2000 to 2015 ($p= 0.0068$), but annual total abundance and richness did not change significantly from one year to the next (Appendix 1)

Reef types clearly changed among years (Appendix 2). In 2000, RC composition differed from CPS, LMR, and LOR, while LIR differed from CPS and LOR. CPS was the only reef type that differed significantly in 2005, while both RC and CPS differed from each other and all other reef types in 2010. In 2015 RC differed from LOR, while LMR and LOR differed from each other. In addition, CPS differed significantly from all other reef types in 2015. Depth proved to be as important as reef type, if not more. The LIR, LMR and LOR all included sites 9 m or deeper and had similar sponge compositions. Also, CPS sites FTL5 and POMP5, shared more species with the deeper linear reef sites than with the other shallow CPS sites (Figure 12).

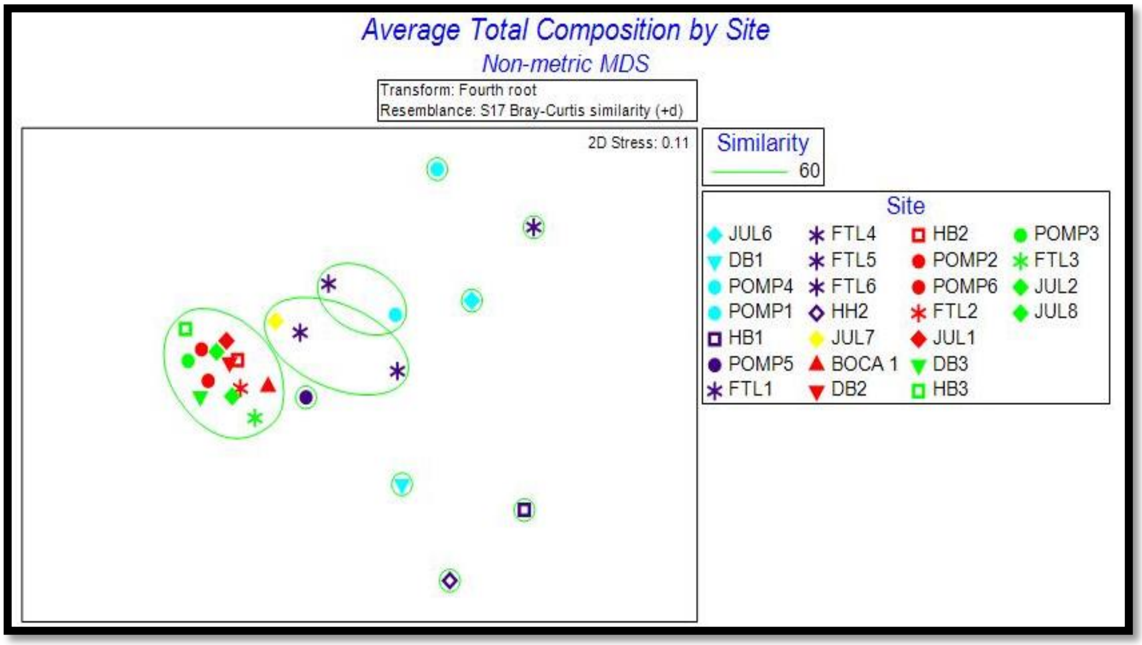


Figure 11: nMDS of Bray-Curtis Similarity index by site. Sites are color coded by reef type: Shallow Ridge (RC) (blue), Colonized Pavement Shallow (CPS) (purple), Linear Inner Reef (LIR) (yellow), Linear Middle Reef (LMR) (red), and Linear Outer Reef (LOR) (green).

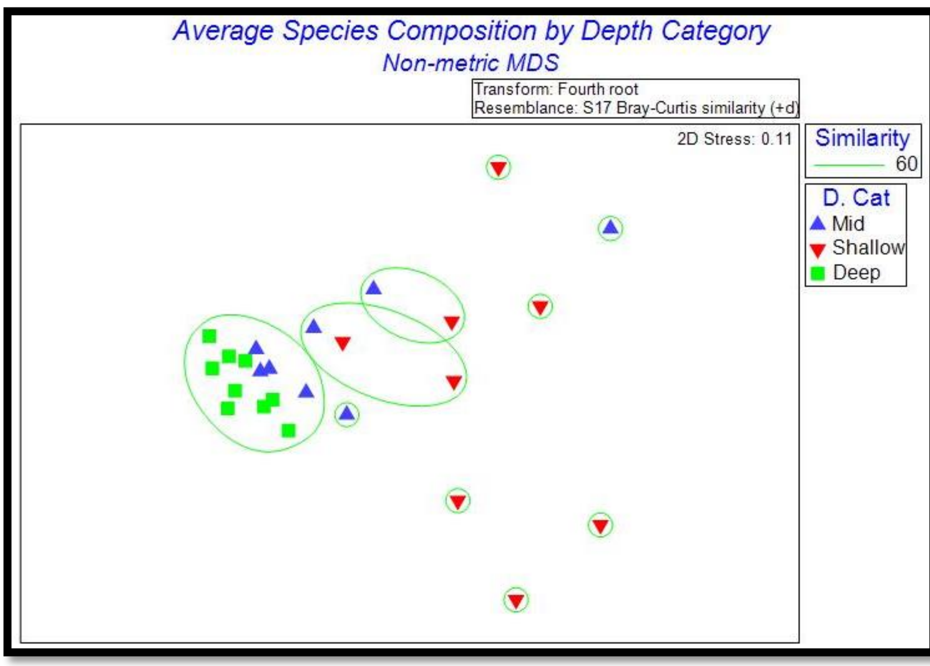


Figure 12: nMDS of Bray-Curtis Similarity. Each point represents the average species composition at different sites and broken down into depth categories: shallow (red) 0-8m, middle (blue) 8.1-14 m, and deep (green) 14.1-18.5 m.

*Table 4: Results of the three-way PERMANOVA. ** in source note the unbalanced design and sites that are missing years. Yellow highlights significance and green highlights the high Pseudo-F, implying high variation between reef types.*

PERMANOVA table of results

Source	df	SS	MS	Pseudo-F	P(perm)	perms
Year	14	62600	4471.4	3.9729	0.0001	9837
Reef	4	1.8789E+06	4.6973E+05	417.35	0.0001	9907
Site (Reef)	20	1.6621E+06	83104	73.838	0.0001	9769
Year x Reef	56	88328	1577.3	1.4014	0.0001	9619
Year x Site (Reef)**	272	3.6691E+05	1348.9	1.1985	0.0001	9230
Res	3670	4.1306E+06	1125.5			
Total	4036	8.2351E+06				

3.1.3 Analysis of Sponge Composition by Reef Type.

Shallow Ridge (RC)

The Shallow Ridge encompassed four of the 25 sites studied. Depth ranged from 3.66 (JUL6) to 6.1 m (POMP 4). It can be characterized as a shallow hard bottom veneered with sand and covered by algae and scattered sponges. It supported the fewest species (10 in 2010 to 18 in 2002, 2004, and 2005) and lowest abundances (63 in 2013 to 168 in 2003) (Figure 13). Common species included; *Aplysina insularis* (average 27 y^{-1}), *Ircinia felix* (8), *Scopalina ruetzleri* (4) and *Ircinia campana* (3) (Figure 14). Species diversity indices declined gradually from 2000 to 2015, with a few abrupt changes in 2001-2002, 2005-2006, and 2008-2011 (Table 5). These changes matched significant changes in sponge composition.

Table 5: Shallow Ridge total richness(s), Abundance (N), Evenness (J'), Shannon-Weiner Index (H') and Simpson's Diversity Index (1-Lambda') 2000-2015.

Year	S	N	J'	H'(loge)	1-Lambda'
2000	14	86	0.8009	2.11362	0.851436
2001	14	78	0.854644	2.255455	0.881785
2002	18	103	0.850841	2.459246	0.897963
2003	16	168	0.705688	1.956583	0.780368
2004	18	92	0.783308	2.26405	0.861443
2005	18	107	0.77133	2.271135	0.864045
2006	14	74	0.724348	1.911596	0.79415
2007	15	87	0.738521	1.999952	0.810478
2008	13	85	0.791147	2.029251	0.834174
2010	10	74	0.714346	1.644843	0.7301
2011	17	98	0.750704	2.126903	0.816537
2012	15	83	0.80203	2.171938	0.838966
2013	12	63	0.797129	1.980791	0.807988
2014	14	68	0.781907	2.063497	0.817384
2015	14	71	0.769863	2.031713	0.811268

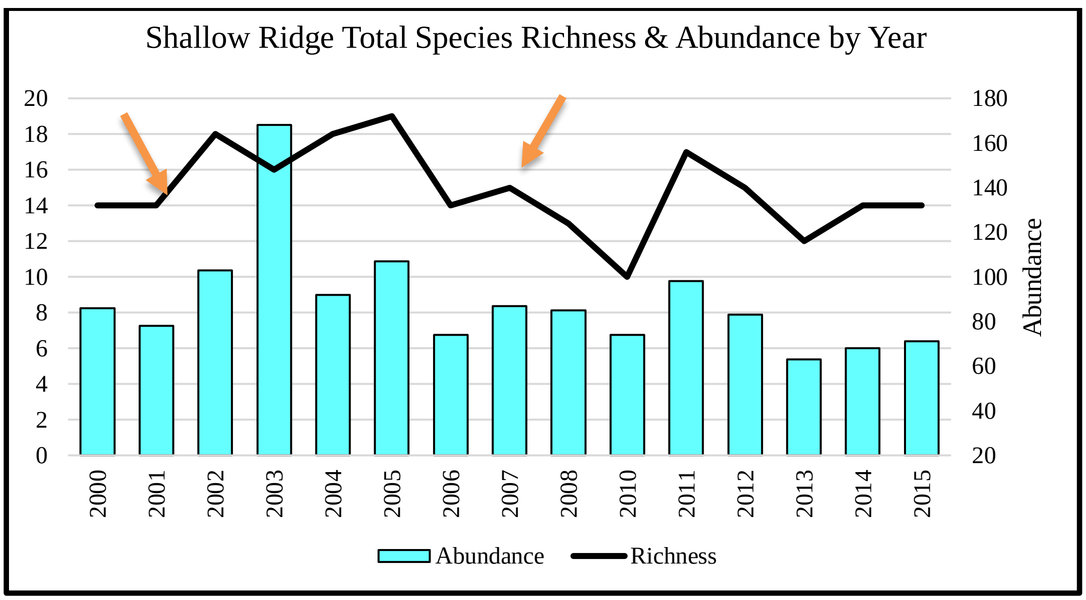


Figure 13: Shallow Ridge total species richness and abundance by year. Orange arrows indicate significant change in species composition between years.

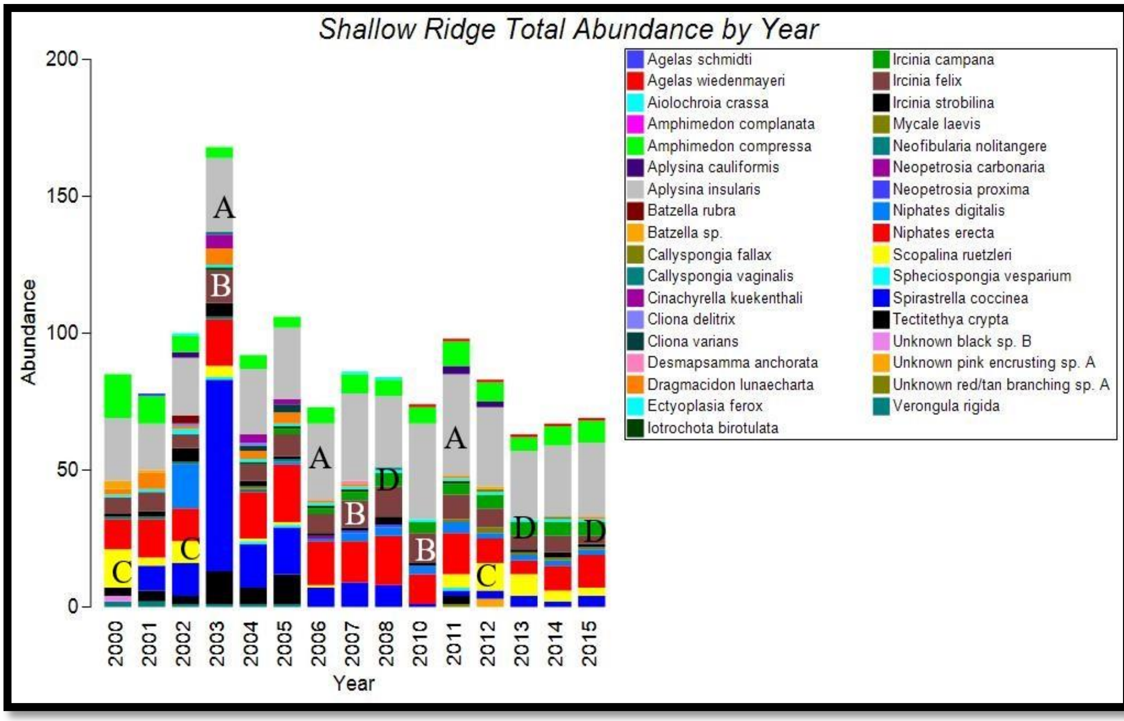


Figure 14: Stacked barplot of total abundance of each species on the Shallow Ridge by year. Note common species of interest: ***A:*** Aplysina insularis *(grey)* ***B:*** *Ircinia felix (brown)* ***C:*** Scopalina ruetzleri *(yellow).* ***D****:* Ircinia campana *(green).*

PERMDISP results yielded significant change between years, but only 2001- 2002 (p=.00424) and 2005-2006 (p=0.0109) had a significant annual change, highlighted in Figure 12 (Appendix 3). Abundance and richness increased substantially but not significantly from 2010 to 2011. Site DB1 contributed most to the difference (p=0.0001) (Appendix 3a). In 2006, the site was buried by sediment with only scattered algae and octocorals remaining. The site remained covered until 2011, when a few sponges became visible. However, the site was buried again by 2012 and remained so until the end of the study. The nMDS plot in Figure 15 shows that site DB1 shared less than 40% similarity with the other three RC sites (JUL6, POMP1, and POMP4); the red point with the blue box around it highlights the buried years 2006-2010, 2012-2015.

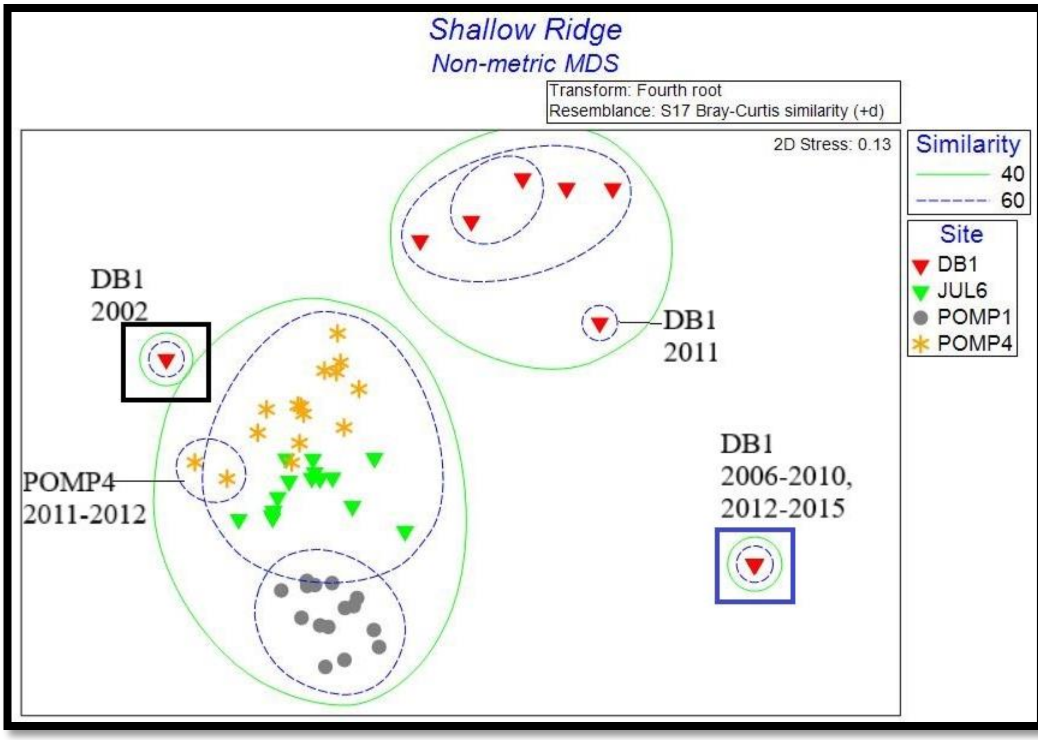


Figure 15: nMDS of Bray-Curtis Similarity of Shallow Ridge sponge assemblage composition. Each point represents a year and site. Green circles mark 40% similarity and blue circles mark 60%, generated by the nMDS to reflect differences versus similarities among sites and years. The blue box marks the overlapped points of DB1 years 2006-2010, 2012-2015, when the site was buried. Note DB1 from 2002 in the black box.

The site was not buried during the 2002 survey and appears as an outlier at 40% similarity surrounded by a black box. Community composition at the other three RC sites were more similar to each other than to DB1 in any year and showed no significant changes in assemblage composition between 2000 and 2015. Interestingly, JUL6 and POMP4 shared higher similarity than POMP1 and POMP4.

Colonized Pavement Shallow (CPS)

Seven sites were located on CPS, and depth ranged from 5.79 (HH2) to 9.45 m (POMP5). The habitat is hard bottom with a thin layer of sediment. Small, encrusting and rope/runner morphotypes dominated, while sponges exhibiting the vase morphotype types were short. Richness ranged from 24 (2000) to 38 (2004) species and abundance from 264

(2000) to 514 (2003) (Figure 16). Common species included *Cliona varians* (average 47 y^{-1}), *S. ruetzleri* (21), *Ap. insularis* (17), and *Iotrochota birotulata* (12) (Figure 17). Species richness gradually increased until 2004 and abundance fluctuated from year to year beginning in 2003 (Figure 16). All diversity indices fluctuated over the study period, with a significant decreased from 2008 to 2010 (Table 6).

Table 6: Shallow colonized pavement richness(s), Abundance (N), Evenness (J'), Shannon-Weiner Index (H') and Simpson's Diversity Index (1-Lambda'), 2000-2015.

Year	S	N	J'	H'(loge)	1-Lambda'
2000	24	264	0.755696	2.401643	0.877232
2001	28	266	0.736943	2.455645	0.878139
2002	32	366	0.766658	2.657034	0.900576
2003	36	514	0.735632	2.636152	0.890262
2004	38	454	0.745075	2.710276	0.899641
2005	33	385	0.791222	2.766514	0.912987
2006	32	356	0.748117	2.592775	0.891439
2007	34	414	0.7592	2.677215	0.900294
2008	34	388	0.766266	2.702132	0.905498
2010	31	316	0.730918	2.509962	0.883102
2011	34	364	0.730492	2.575978	0.891714
2012	32	372	0.748825	2.595229	0.893995
2013	29	461	0.785231	2.644106	0.908564
2014	28	430	0.759509	2.530838	0.895105
2015	26	483	0.753878	2.456206	0.887022

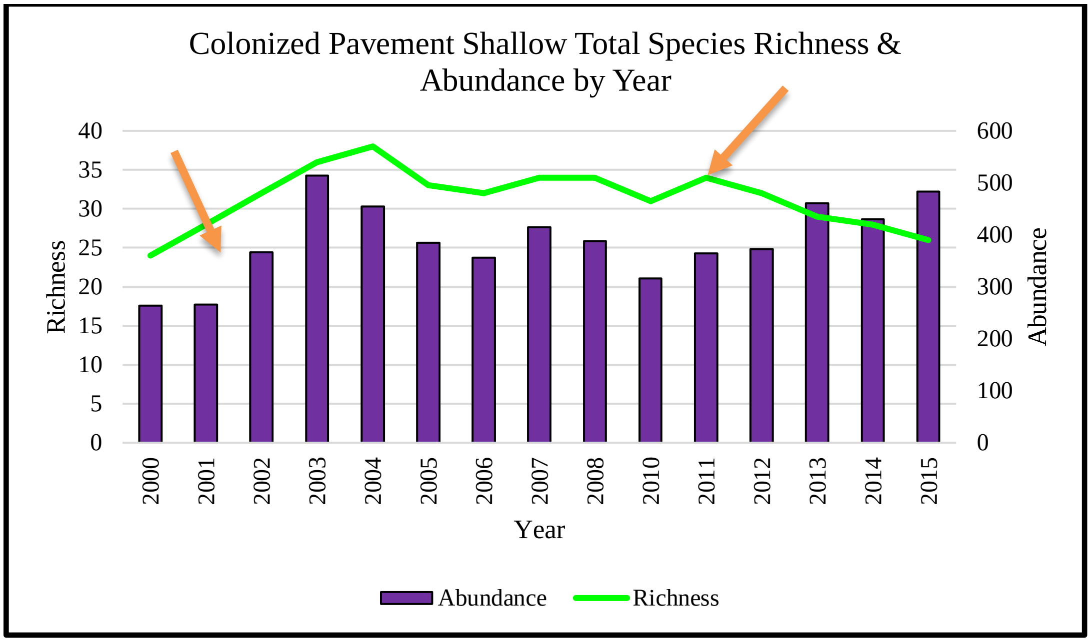


Figure 16: Shallow Colonized Pavement total species richness and abundance by year. Orange arrows indicate years with significant change.

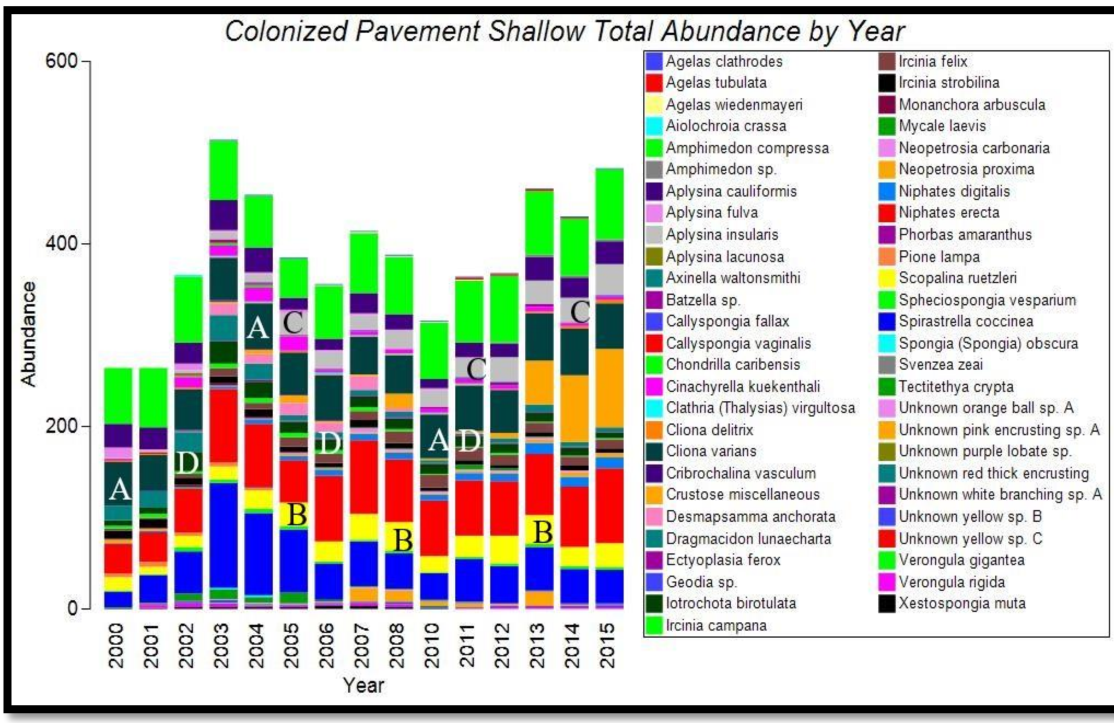


Figure 17: Shallow Colonized Pavement total abundance by year. Note common species. ***A:*** Cliona varians *(forest green).* ***B:*** Aplysina insularis *(gray).* ***C:*** Scopalina ruetzleri *(yellow).* ***D:*** Iotrochota birotulata *(dark green).*

PERMDISP by year yielded significant change in species composition from 2000-2015 (p=0.0158), specifically 2001-2002 (p=0.0037) and 2008-2010 (p=0.0474) (Appendix 4). PERMDISP of individual sites revealed that HB1 from 2005-2015 (p=.0001) and FTL6 from 2008-2010 (p=0.0547*) exhibited significant annual changes (Appendix 4a, 4b). FTL1 exhibited significant change from 2000 to 2015 but had no annual significant change. Figure 18 shows that HB1, HH2 and FTL6 support sponge communities that differ from those at FTL1, FTL4, FTL5, and POMP5, which clustered together in all years at 40%. However, at 60% similarity the distinction in species composition is clear, e.g., the overlap of FTL1 in 2005-2007 and in 2015 with FTL4 and FTL5. Site HB1 was buried in 2006, was uncovered in 2013, and was buried again by 2014. The change in species composition at HB1 is evident in Figure 18; years 2002-2005 share similar species composition with HH2, while 2000 and 2001 had low richness and abundance. Species composition at HB1 alone was extremely low in 2013, the one year it was uncovered, and closer to the buried years (2006- 2012, 2014-2015) than early 2000s. Throughout the study, HB1 and HH2 differed from the other CPS sites. However, unlike HB1, HH2 exhibited no major change over time. The separation of FTL6 years at 60% similarity occurred between 2007 and 2008 with species composition during the earlier years, 2003-2007, closer to that of sites FTL1, 4, 5 and POMP5. In addition, FTL6 was dominated by staghorn coral, *Acropora cervicornis*, covered in a combination of crustose algae and encrusting sponges, which increased in abundance over time and made identification of sponges to species from photos nearly impossible. It also drove the difference in species composition of this site relative to all other sites.

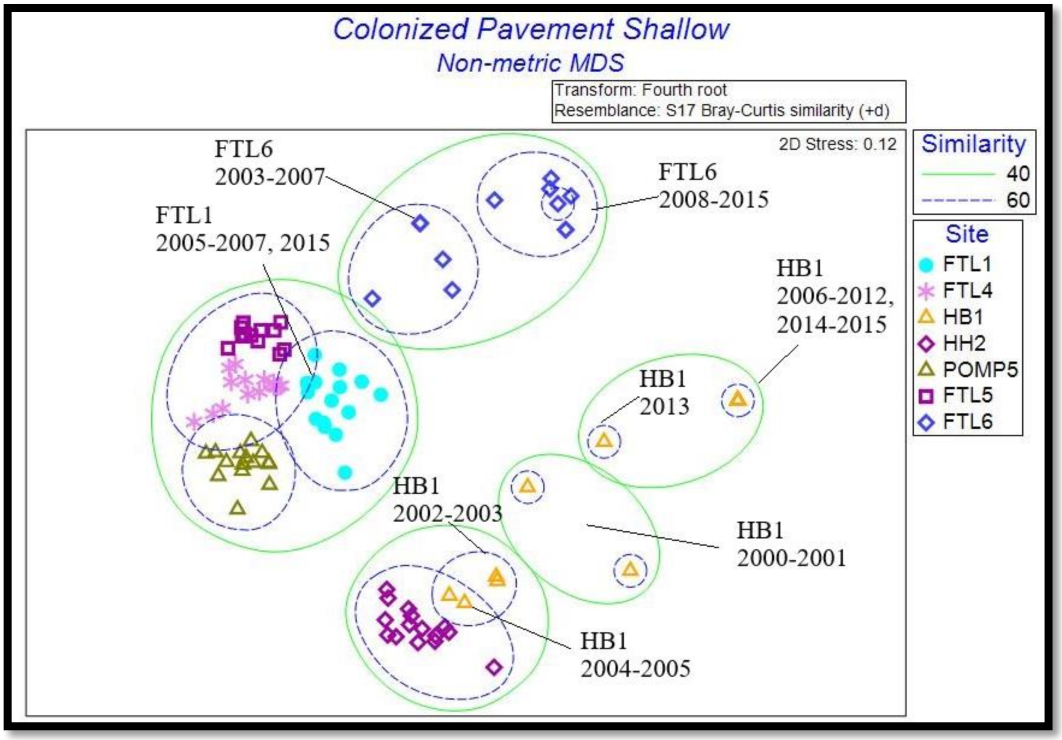


Figure 18: nMDS of Bray-Curtis Similarity of Shallow Colonized Pavement. Each point represents a year and site. Green circles mark 40% similarity between the sites and blue marks 60%. Note distinct separation of HB1, HH2 and FTL6 from the other sites.

Linear Inner Reef (LIR)

The habitat at site JUL7, the only site on the LIR (depth of 9.75 m), consisted of low-relief reef formations and short branching and tube sponges. Species richness and abundance were lower than at other reef types. Species richness was lowest (14) in 2013 and highest (19) in 2011. Abundance ranged from 58 in 2014 to 103 in 2008 (Figure 19). The most common species was *Aplysina insularis* (average 7 y^{-1}). Other common species included *Scopalina ruetzleri* (5), *Iotrochota birotulata* and *Xestospongia muta* (4 y^{-1} each) (Figure 20). Diversity indices fluctuated beginning in 2004. LIR had the highest Pielou's Evenness Index of all reef types throughout the study, averaging 0.804005, but the Shannon-Wiener and Simpson's were more similar to the RC than LMR and LOR (Table 7).

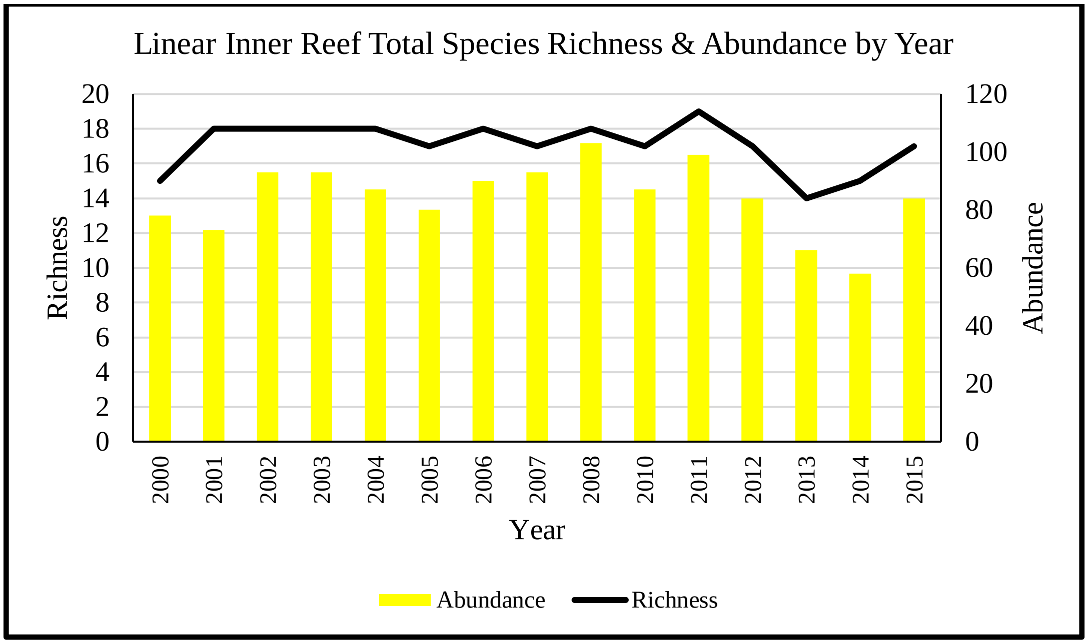


Figure 19: Linear Inner Reef total species richness and abundance by year.

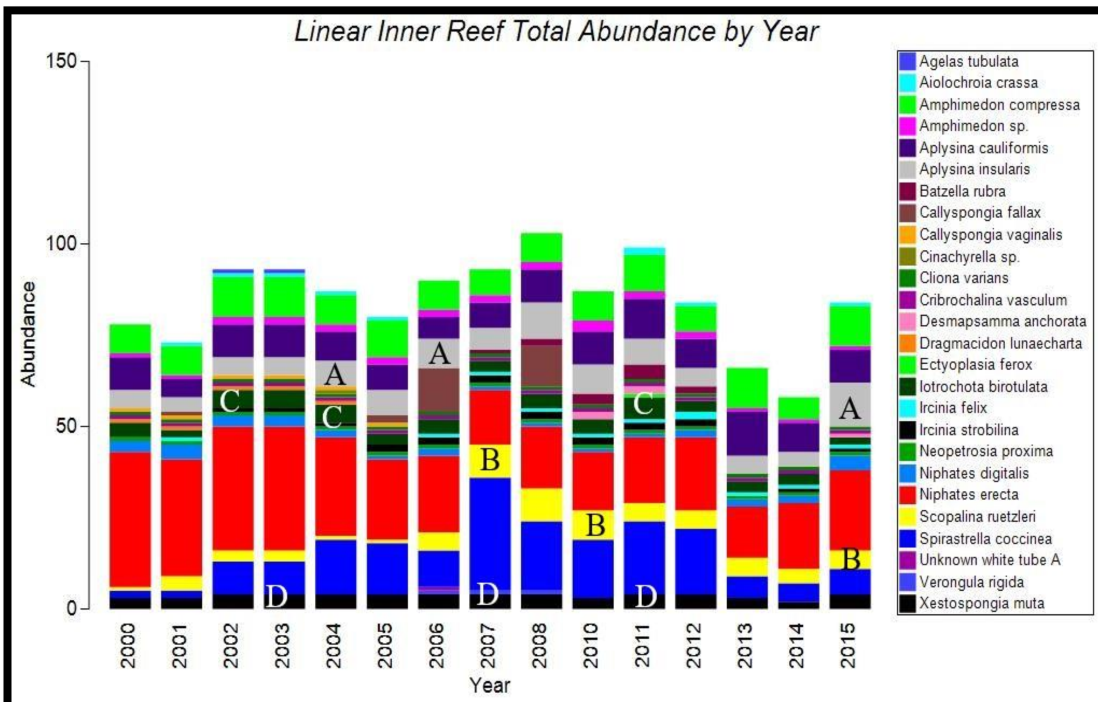


Figure 20: Total abundance on the Linear Inner Reef by year. Note common species. ***A:*** Aplysina insularis *(maroon).* ***B:*** Scopalina ruetzleri *(yellow).* ***C:*** Iotrochota birotulata *(dark green).* ***D:*** Xestospongia muta *(black).*

Table 7: Linear Inner Reef total richness(s), Abundance (N), Evenness (J'), Shannon-Weiner Index (H') and Simpson's Diversity Index (1-Lambda') 2000-2015.

Year	**S**	**N**	**J'**	**H'(loge)**	**1-Lambda'**
2000	15	78	0.701794	1.900493	0.749251
2001	18	73	0.734196	2.1221	0.788052
2002	18	93	0.766695	2.216033	0.831463
2003	18	93	0.766695	2.216033	0.831463
2004	18	87	0.778122	2.249061	0.852713
2005	17	80	0.804492	2.279299	0.866772
2006	18	90	0.849122	2.454279	0.89588
2007	17	93	0.778308	2.205113	0.84245
2008	18	103	0.847913	2.450783	0.900628
2010	17	87	0.85977	2.435911	0.899225
2011	19	99	0.838829	2.469881	0.895898
2012	17	84	0.832487	2.358613	0.877797
2013	14	66	0.852874	2.250785	0.881585
2014	15	58	0.83332	2.256671	0.865094
2015	17	84	0.815454	2.310354	0.876076

Linear Middle Reef (LMR)

The Linear Middle Reef encompassed seven of the 25 sites and ranged in depth from 9.14 (BOCA1) to 15.58 m (POMP6). The habitat was hard bottom with high diversity of sponges, stony corals, and soft corals. Photoquadrats showed intense competition for space, and morphologies varied. Richness ranged from 41 in 2003-2004 and 2014-2015 to 46 in 2010. Abundance ranged from 962 in 2012 to 1031 in 2001 (Figure 21). Both abundance and species richness diminished substantially from 2013 to 2014 (Figure 21). Abundant species included *Niphates digitalis* (average 38 y^{-1}), *Scopalina ruetzleri* (34), *Iotochota birotulata* and *D. anchorata* (33 y^{-1} each), *Ircinia strobilina* (25), and *Aiolochroia crassa* (22) (Figure 22). LMR showed high diversity and evenness from 2000-2015, with a decrease in Simpson's Diversity Index (1-Lambda') (Table 8).

Table 8: Linear Middle Reef total richness(s), Abundance (N), Evenness (J'), Shannon-Weiner Index (H') and Simpson's Diversity Index (1-Lambda') 2000-2015.

Year	S	N	J'	H'(loge)	1-Lambda'
2000	42	1045	0.744084	2.781138	0.90482
2001	44	1031	0.744575	2.817612	0.912619
2002	43	1026	0.724487	2.724942	0.894526
2003	41	1147	0.710946	2.640148	0.885345
2004	41	1131	0.701134	2.60371	0.877314
2005	42	1049	0.698661	2.611363	0.875601
2006	44	1012	0.708806	2.682257	0.886869
2007	45	1140	0.701913	2.671946	0.889176
2008	44	1128	0.703274	2.661321	0.885419
2010	46	1130	0.70808	2.710986	0.890532
2011	45	1060	0.710584	2.704955	0.886951
2012	44	962	0.681854	2.580264	0.869259
2013	45	1146	0.68752	2.617155	0.876458
2014	41	1060	0.692242	2.570689	0.878256
2015	41	1063	0.690799	2.565334	0.878227

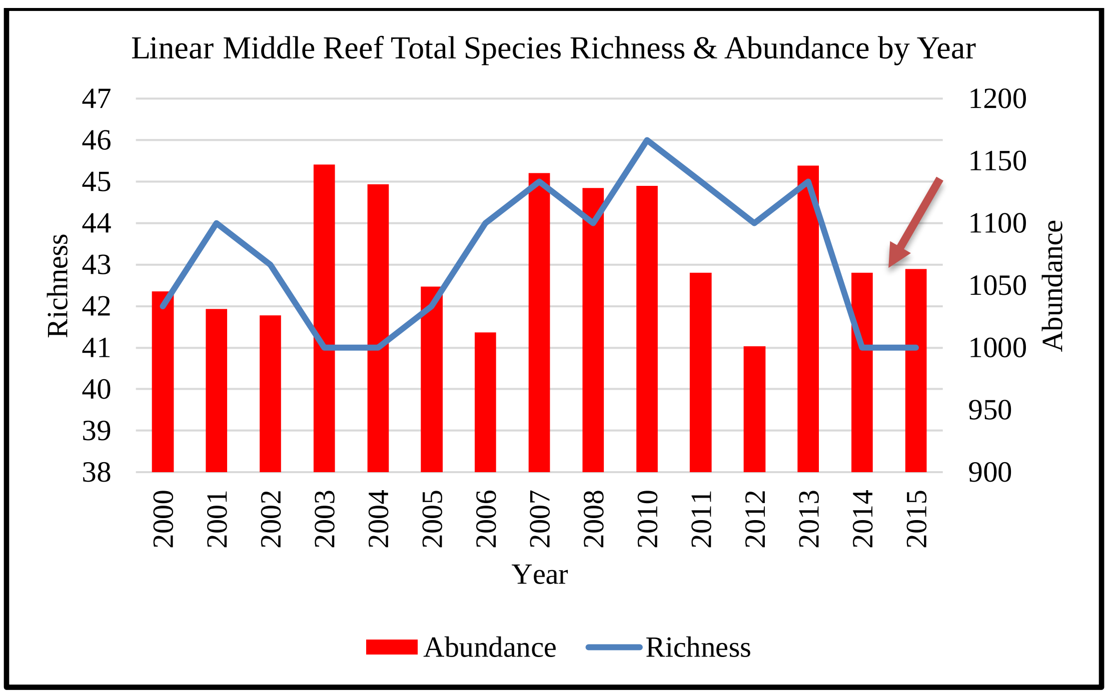


Figure 21: Total Linear Middle Reef abundance and species richness by year. Orange arrow indicates significant annual change.

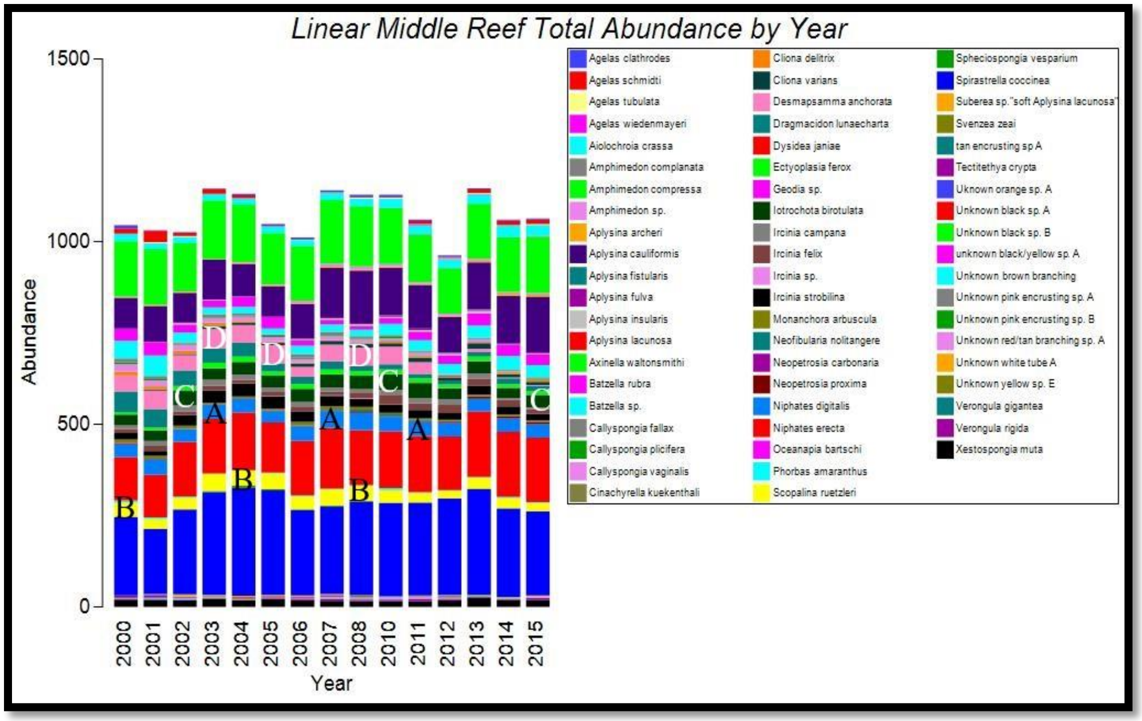


Figure 22: Stacked barplot of total LMR abundance by year. Note common species: ***A:*** Niphates digitalis *(light blue),* ***B:*** Scopalina ruetzleri *(yellow),* ***C:*** Iotrochota birotulata *(dark green), and* ***D:*** Desmapsamma anchorata *(light pink).*

PERMDISP results yielded significant change from 2000 to 2015 (p= 0.0001) (Appendix 5). The only significant change from one year to the next was 2013-2014 (p=0.0489), which can be attributable to the removal of site BOCA1 from the project. Sites DB2 (p=0.0465) and FTL2 (p=0.0002) were the only sites at which sponge composition changed significantly from 2000-2015, although neither showed any significant change between successive years (Appendices 5a, b). The nMDS plot highlights the 60% similarity in species composition among the LMR sites across all years, except for BOCA1, which only shared partial similarity with the other sites from 2002 to 2004 and 2007, 2008, 2012, 2013 (Figure 23). The change in species composition at BOCA1 can likely be attributed to the 2004 and 2005 hurricanes.

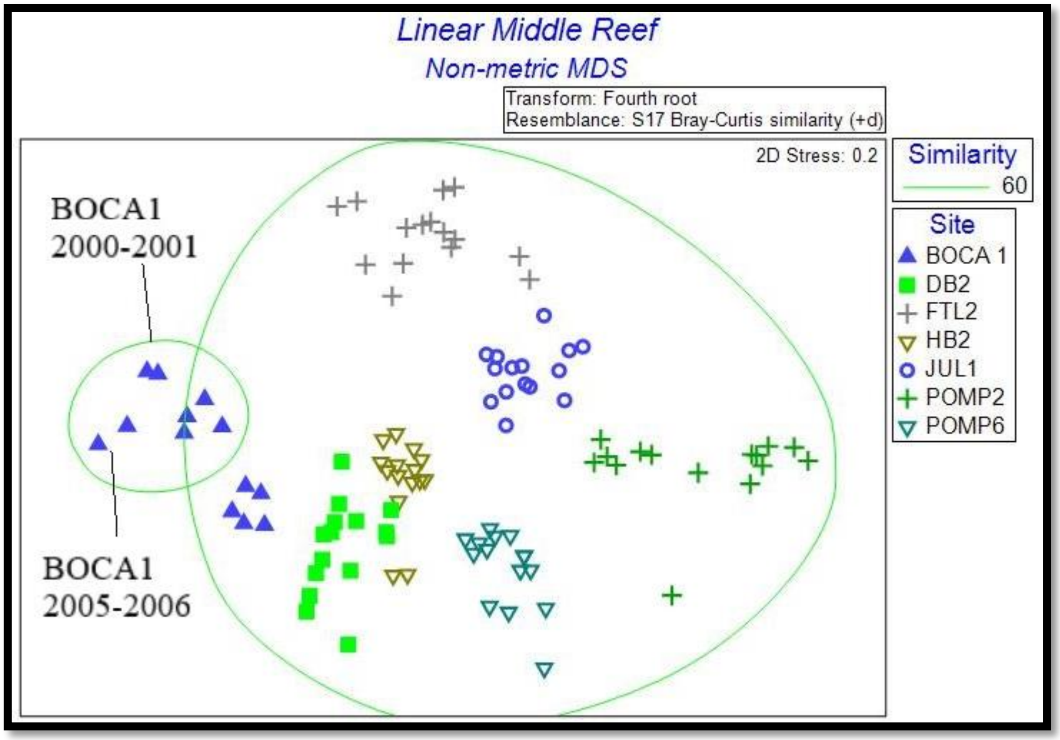


Figure 23: nMDS of Bray-Curtis Similarity of the Linear Middle Reef. Each point represents a site and year. The green circles represent 60% similarity.

Linear Outer Reef (LOR)

The Linear Outer Reef included six sites ranging in depth from 14.93 (HB3) to 18.29 m (FTL3). This is a highly productive reef habitat with sponge morphotypes ranging widely, from encrusting to massive. Richness ranged from 34 species in 2000 to 44 in 2015 and abundance from 635 in 2001 to 980 in 2015 (Figure 24). Common species included *Batzella rubra* (71 y^{-1}), *Scopalina ruetzleri* (68), *Niphates digitalis* (46), *Xestospongia muta* (27 y^{-1}), and *Aiolochroia crassa* (12) (Figure 25). This reef type had the highest diversity indices but lower species richness and abundances than the Linear Middle Reef (Table 7). Richness and abundance gradually increased from 2000 to 2015.

Table 9: Linear Outer Reef total richness(s), Abundance (N), Evenness (J'), Shannon-Weiner Index (H') and Simpson's Diversity Index (1-Lambda') 2000-2015.

Year	S	N	J'	H'(loge)	1-Lambda'
2000	36	657	0.762589	2.732754	0.911539
2001	38	635	0.745131	2.710477	0.906416
2002	35	872	0.718709	2.55526	0.884157
2003	34	933	0.71501	2.521384	0.877692
2004	38	881	0.716428	2.606068	0.885995
2005	39	905	0.736176	2.697026	0.893226
2006	38	805	0.755418	2.747897	0.903544
2007	39	912	0.748908	2.743669	0.902043
2008	39	894	0.746067	2.733263	0.903087
2010	39	852	0.738678	2.706193	0.902956
2011	38	895	0.739729	2.690828	0.900901
2012	42	967	0.739645	2.764548	0.907368
2013	43	954	0.744837	2.80148	0.91178
2014	42	948	0.74045	2.767559	0.909176
2015	44	980	0.723625	2.738334	0.903596

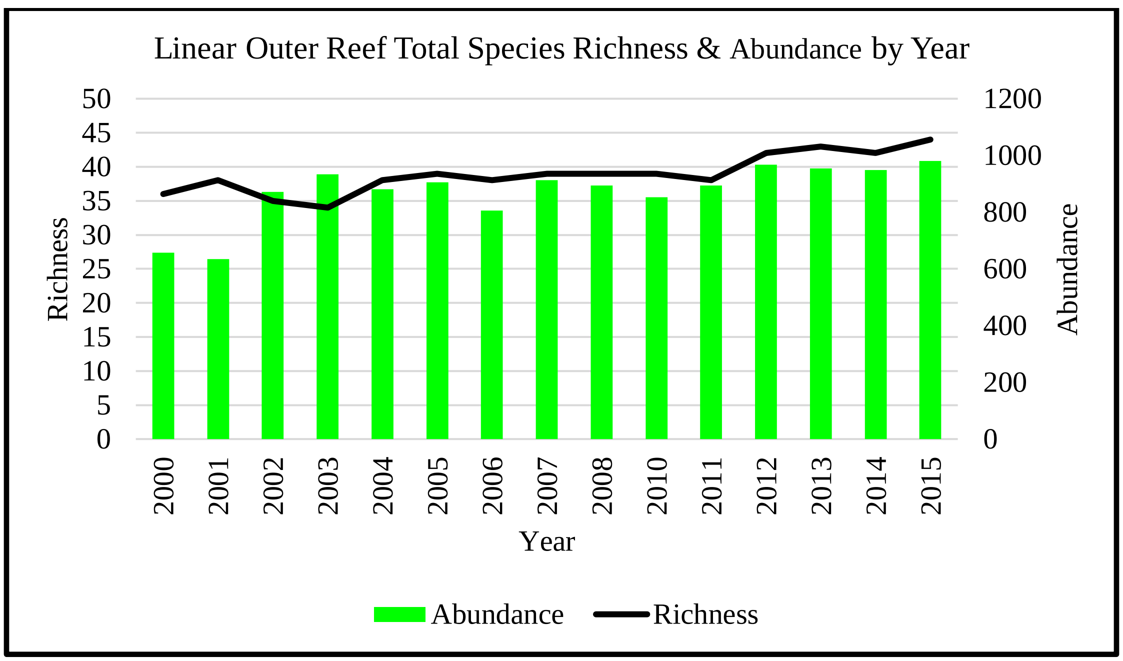


Figure 24: Linear Outer Reef total species richness and abundance by year. No significant annual changes were recorded between any years.

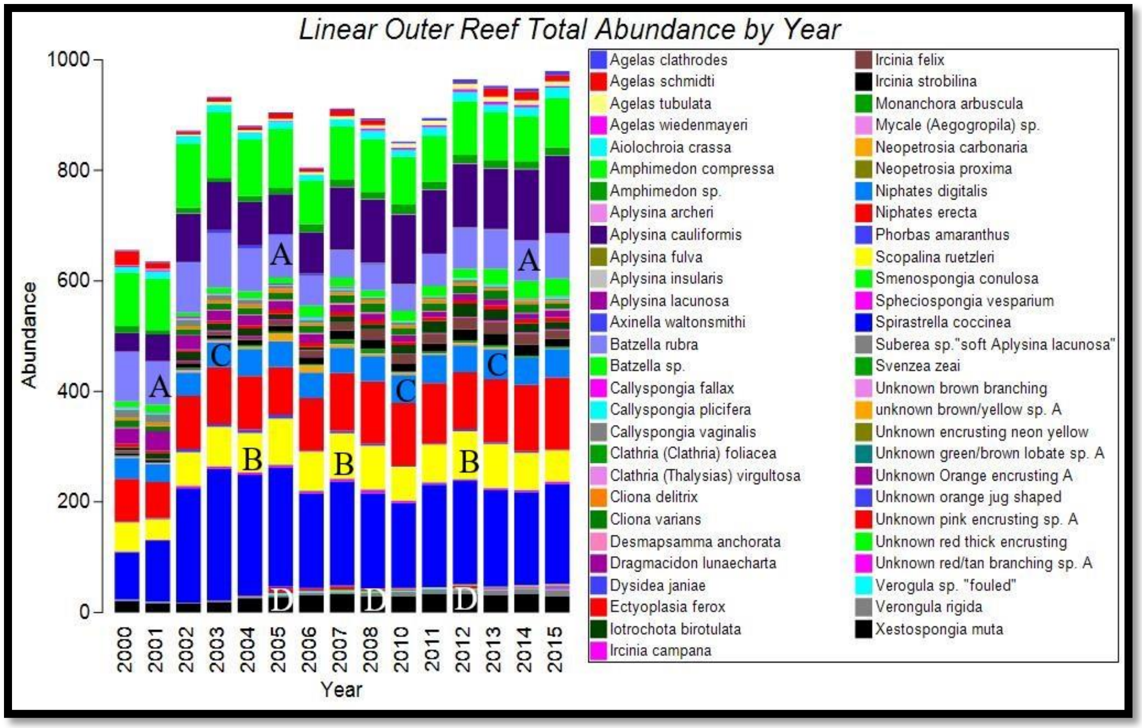


Figure 25: Stack bar plot of Linear Outer Reef total abundance by year. Common species include ***A:*** Niphates digitalis *(light blue)* ***B:*** Batzella rubra *(light purple)* ***C:*** Scopalina ruetzleri *(yellow)* ***D:*** Xestospongia muta *(black). Note the gradual increase in abundance overtime.*

Assemblage composition changed significantly overall at LOR sites from 2000 to 2015 (p=0.0001), with the change specifically between 2001 and 2005 (p=0.0001) (Appendix 6). Composition changed significantly between years at POMP3 in 2002-2003 (p=0.0414) and at DB3 in 2001-2002 (p=0.0028) and 2007-2008 (p=0.0291) (Appendices 6a, b). Although the PERMDISP was significant, and the nMDS plot shows all annual values clustering separately by site, the clustering of all sites and years within the 60% similarity circle reflects an overall lack of variation in the sponge community (Figure 26). This implies that abundance changed over time, but species richness did not.

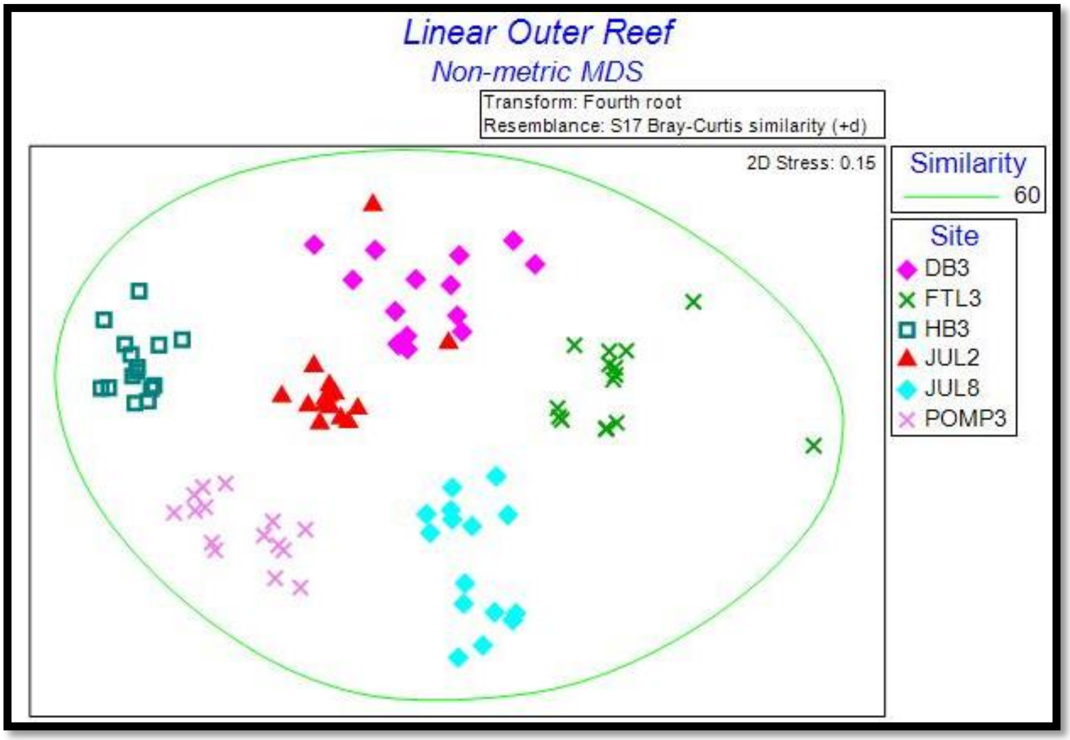
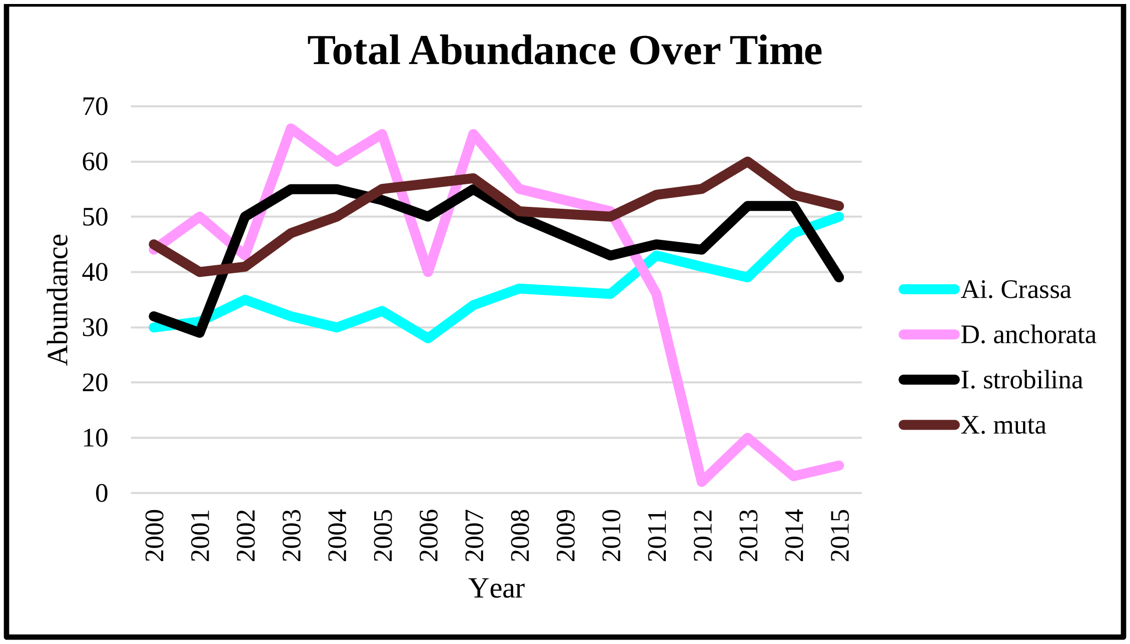


Figure 26: nMDS of Bray-Curtis Similarity of Linear Outer Reef composition. Each point represents a site and year. Dotted green line represents 60% similarity.

3.2 Hypothesis Two

Individual species were chosen based on their frequency of appearance, different morphologies, and ease of measurement in photographs. Two species (*Amphimedon compressa,* and *Ircinia strobilina*) decreased in abundance from 2004 to 2006, whereas *Aiolochroia crassa* and *Desmapsamma anchorata* decreased in abundance from 2003 to 2004 and increased in 2005 before decreasing again in 2006, and *Xestospongia muta* recorded a slight increase in abundance (Figure 27) and size. In addition, all species declined in abundance at least slightly from 2009 to 2010. However, whereas three then increased in 2011, *D. anchorata* decreased dramatically from 2010 to 2012, and *Am. compressa* declined only to 2011.



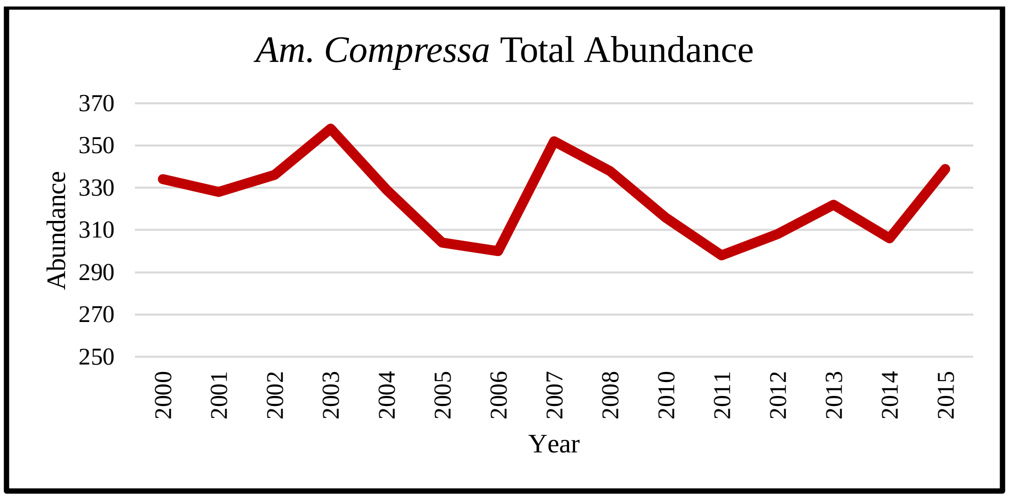


Figure 27: Total abundance of five common species over time. Amphimedon compressa *is graphed separately due to its substantially greater abundance*. *(Note differences in vertical scales.)*

lme regressions plotted as ggplots scatterplots (Figures 28, 29) show variations in species area within quadrats over time. *Desmapsamma anchorata* exhibited the only annual significant change in area—a downward trend—whereas *Ai. crassa, I. strobilina, and X. muta* increased in area over time (Appendix 9). The differences may be related to their lifespans. For example, *X. muta* generally survived the length of the study, while *D. anchorata* survived on average for two years. Longevities of individuals of *Ai. crassa* and

I. strobilina were more difficult to assess, as many were large and at least several years old at the beginning of the study. In addition, both species had new recruits towards the end of the study. Nevertheless, longevities of *Ai. crassa* and *I. strobilina* clearly fall between the two extremes of *X. muta* and *D. anchorata.* This is supported by the results of the *Tukey's post-hoc* analyses on the three massive morphotypes (*Ai. crassa, I. strobilina,* and *X. muta*), which revealed overall trends of lower p-values between early years (2000-2006) and 2015, implying that these species grew during the study and that mortality of some individuals was compensated by growth of the remaining individuals (Figure 28) (Appendices 7, 10, 11). In addition, *D. anchorata* p-values were consistently lower than the other species, reflecting its shorter lifespan.

Amphimedon compressa was by far the most common species but exhibited no significant change in area over time (Figures 28, 29). However, visual observations revealed substantial change over time associated with natural events. Partial mortality in this species, in which pieces of an individual break off and may or may not reattach to the substrate to continue growing, perhaps offset recruitment of new individuals to produce a near linear average area (Figure 29B).

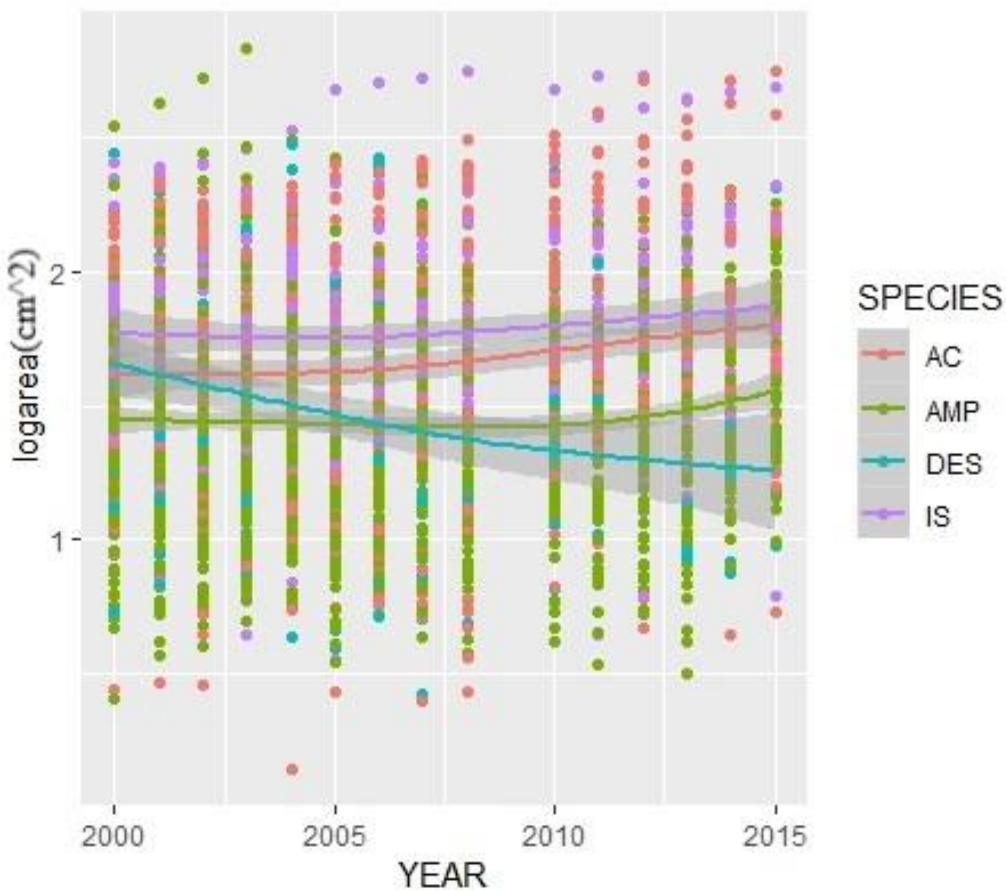


Figure 28: Scale transformed scatter ggplot of Aiolochroia crassa *(AC),* Amphimedon compressa *(AMP),* Desmapsamma anchorata *(DES) and* Ircinia strobilina *(IS) over time. Grey area around each line represents a 95% confident interval*. Xestospongia muta *was excluded from the figure due its substantially much larger area (see figure 29 below).*

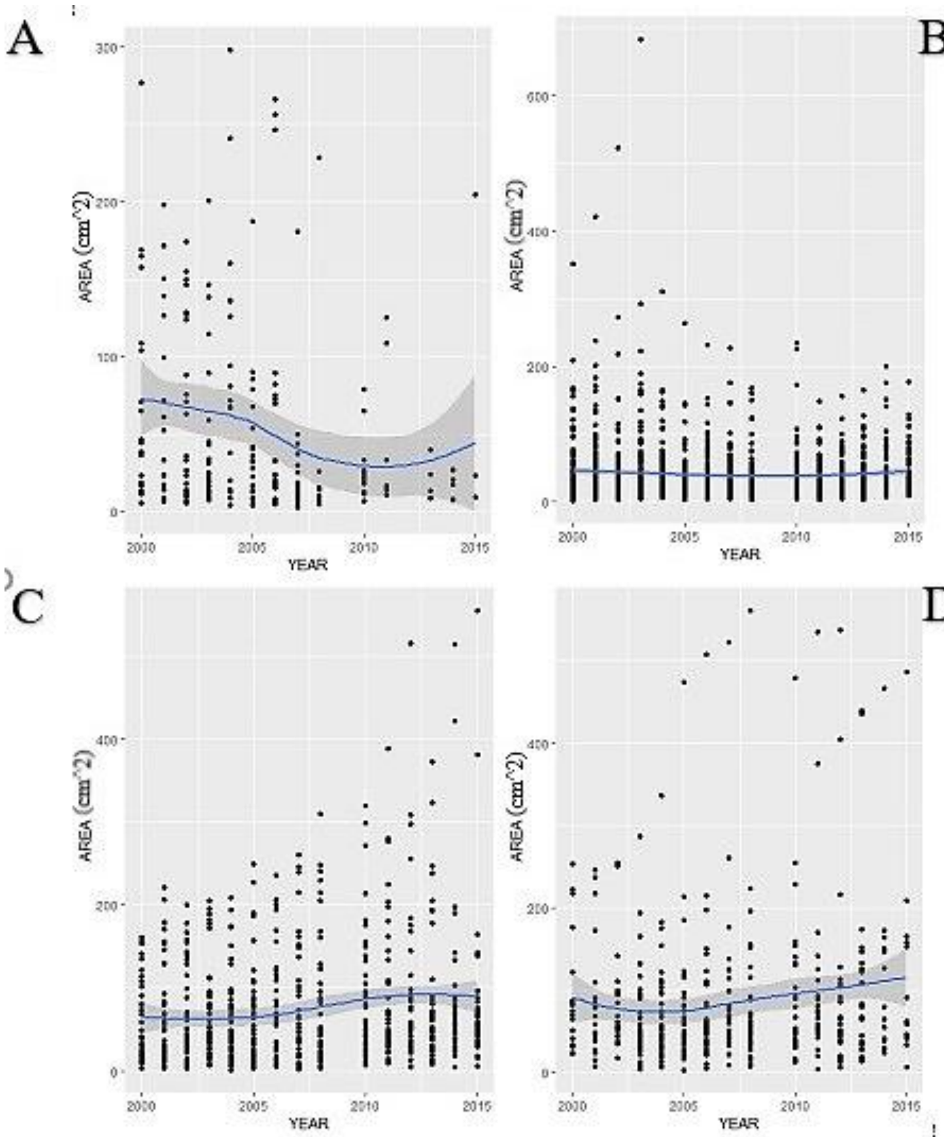


Figure 29: Scatter ggplots of area of each species over time. ***A:*** D. anchorata, ***B:*** Am. compressa, ***C:*** Ai. crassa, ***D:*** I. strobilina. *Note that the Y-axis for* D. anchorata *is half that of the other species.*

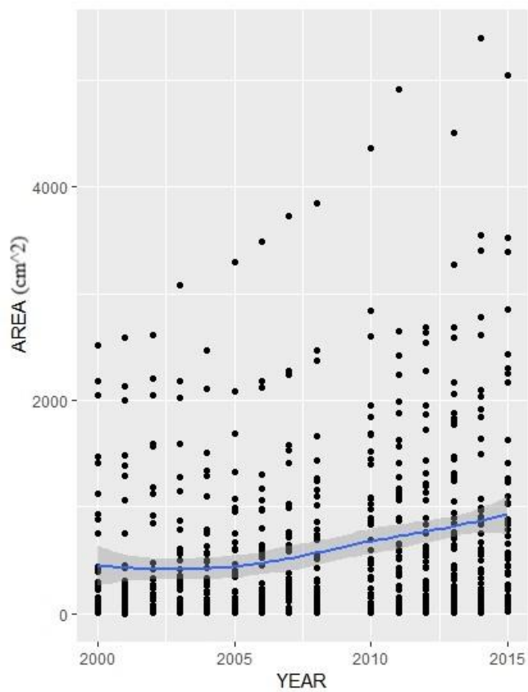


Figure 29 continued: Scatter ggplot of X. muta *over time. Note that the Y-axis is at a scale ten times that for* Ai. crassa, I. strobilina*, and* Am. compressa*, and 20 times that for* D. anchorata.

4. Discussion

4.1 Hypothesis One

This study examined the composition, abundance and distributions of sponge assemblages in a variety of habitats along the SEFRT in Broward County from 2000 to 2015 based on images provided by the Broward County annual monitoring project of local reef communities. Overall sponge composition remained relatively constant over time but with some fluctuations. However, different reef types and sites within them showed significant differences and trends in richness and abundance, reflecting different driving spatial and temporal factors, i.e., differing environmental conditions, as well as both anthropogenic and natural events such as the decline in *Tethya crypta* following Hurricane Wilma in 2005.

The Shallow Ridge (RC) differed from the other reef types significantly and consistently, most likely due to its shallow, near-shore location influenced by the physics of shoreline factors, and frequently burial by sediment. Sites were often subject to heavy sedimentation and turbid waters, leading to low species richness and domination by encrusting or small species. Richness ranged from 10 (2010) to 18 (2002, 2004 - 2005); Shannon-Wiener diversity from 1.644843 (2010) to 2.459246 (2002) and abundance from 63 (2013) to 168 (2003).

The Shallow Colonized Pavement (CPS) differed significantly from all other reef types in 2005 and all but LIR in 2010. The CPS is flat, carbonate rock with variable coverage, dominated by rope/runner and short vase morphotypes. Richness ranged from 24 (2000) to 38 (2004), diversity from 2.401643 (2000) to 2.91222 (2005), and abundance 264 (2000) to 514 (2003).

The Linear Inner Reef consists of immature reef formations and was dominated by short branching and tube sponges. Pielou's evenness was high throughout the study, while diversity ranged from 1.900493 (2000) to 2.469881 (2011). Richness ranged from 14 (2013) to 19 (2011) and abundance 58 (2014) to 103 (2008). Because only one site was located on the LIR, richness and abundance values were lower throughout the study.

The Linear Middle Reef is a highly diverse environment with the largest sponge diversity and abundance in this study. Sponge assemblages resembled those at the LOR and LIR sites. Richness ranged from 41 (2003-2005, 2014, 2015) to 46 (2010), diversity from 2.565334 (2001) to 2.817612 (2002), and abundance 962 (2012) to 1147 (2003).

Sites on the Linear Outer Reef were the deepest and exhibited a continuous increase in richness diversity and abundance during the study. Richness ranged from 34 (2003) to 44 (2015), diversity 2.9080275 (2003) to 3.0892856 (2013), and abundance from 635 (2001) to 980 (2015). LOR richness, diversity, and abundance significantly differed from the CPS throughout the study and resembled those of the LMR.

4.1.1 Sedimentation, turbidity and beach renourishment

Few sponge species are adapted to survive in heavily turbid environments (Cerrano, 2004; Pineda *et al.*, 2017). Heavy sedimentation may result in clogging of ostia and oscules, reducing filtration ability and thus energy available for reproduction (Wulff, 2013; Bell *et al.*, 2015). However, the occurrence of sedimentation events, such as beach renourishment and hurricanes, within the same year required examination of changes within each site.

It is a concern that dredged sand from select offshore sites will adversely affect nearby reefs by suspending sediment in the water column and potentially smothering organisms (Dodge *et al.*, 1989; Dodge *et al.*, 1991a; Dodge *et al.*, 1991b; Fisher *et al.*, 2008). Broward County renourished several beaches between 2000 and 2015. Between March and April 2011, 340,000 cubic yards of sand were taken from a dredge site only 110 m offshore Deerfield Beach between the first and second reefs (OAI, 2011). Despite this disturbance, the nearby HB and DB sites were not negatively affected. In fact, the shallow site DB1, which had previously been covered by a thick layer of sediment when surveyed from 2006 to 2010, was uncovered in 2011, which led to rapid recolonization before reburial in 2012. As annual surveys took place six months after the renourishment project ended, it is difficult to determine whether the dredging, or another yet unknown factor, was the cause. In addition, it is possible that there were short-term consequences, such as suspending feeding and decreased respiration on deeper sites, but the sponges had since recovered (Bell *et al.*, 2015; Pineda *et al.*, 2017). Southern sites along John Lloyd State Park and Hollywood Beach were renourished twice between 2005-2006 and 2012-2013 (2018). In both instances sand was taken from the nearby Port Everglades spoil shoal on the north side of the Port Everglades Channel entrance, and no major adverse effects on the sponge community was seen (OAI, 2011). As with to the northern sites HB and DB, the southern sites JUL and HH were not surveyed until several months after renourishment.

4.1.2 Hurricanes

Natural events such as hurricanes often shape the structure of reefs (Powell and Houston, 1996; Wilkinson, 2008; Wulff, 2013). Tropical storms and hurricanes frequently impact southeastern Florida, which experienced nine tropical storms and five hurricanes between 2000 and 2015 alone (NOAA, 2016). Impacts of storms on each reef type and sponge community were difficult to quantify, because weather affected when annual surveys were carried out. Half the sites in 2004 were visited before Hurricanes Frances, Ivan and Jeanne, and 11 of the 25 were visited in 2005 after Hurricane Katrina but before hurricane Wilma, while the remaining thirteen sites were visited in early 2006, several months after Wilma. However, it is clear the storms had a negative impact on the reefs. Across all reef types, branching/tube species such as *A. cauliformis* and *C. vaginalis* decreased in numbers from 239 to 187 and 24 to 15, respectively, from 2004 to 2006. The storms had mixed effects on shallow-water encrusting species: several species decreased in abundance due to smothering (*S. coccinea* from 636 to 463 and *D. lunaecharta* from 78 to 43*)*, whereas several others, such as *C. varians* were unaffected. Visibility of encrusting species was probably due to shifts in sedimentation by storm surges (Cerrano, 2004; Wulff, 2013). Individual massive species were affected by the storms in different ways and reflected trends observed in the Florida Keys (McMurray *et al.*, 2015) and Belize Barrier Reef (Wulff, 2013). *Xestospongia muta* and *I. campana* sustained breakage during storms, and, while the former generally recovered, the latter often died. The shallow sites DB1 and HB1 saw a decrease in abundance following the 2004 storms, with partial recovery by October 2005, but both sites were buried under a thick layer of sediment following the 2005 hurricanes. This was likely a result of sediment shifted from nearby sand shoals, similar to what Wulff (2013) observed at shallow sites in Belize. The volume of sponges that wash ashore following such storms exemplify their destructive capacity (Figure 30).

Figure 30: Mizell-Johnson (formerly John U. Lloyd) State Park beach following Hurricane Irma, showing extensive windrows with abundant dead sponges.

Despite their obviously destructive effects, hurricanes and tropical storms may have positive impacts on reef communities. These storms often clear macroalgae, octocorals, sponges, and other species, including invasives such as the macroalga *Caulerpa brachypus* and the coral *Tubastraea coccinea,* which creates space, reduces competition and permits sponge recruitment (Bell *et al.*, 2017b). Storms may shift sediment and expose buried substrate for recruitment for rapidly colonizing sponges (Wilkinson, 2008). Although not quantified this study, images revealed noticeably fewer algae and octocorals following Hurricane Wilma (Figure 31). Most sites recovered quickly; sites surveyed several months after the storms saw an increase in species richness and diversity, especially on the LMR and LOR. New individuals of species such as *Monanchora arbuscula* and *Aiolochroia crassa* often appeared following storms (Figure 32).

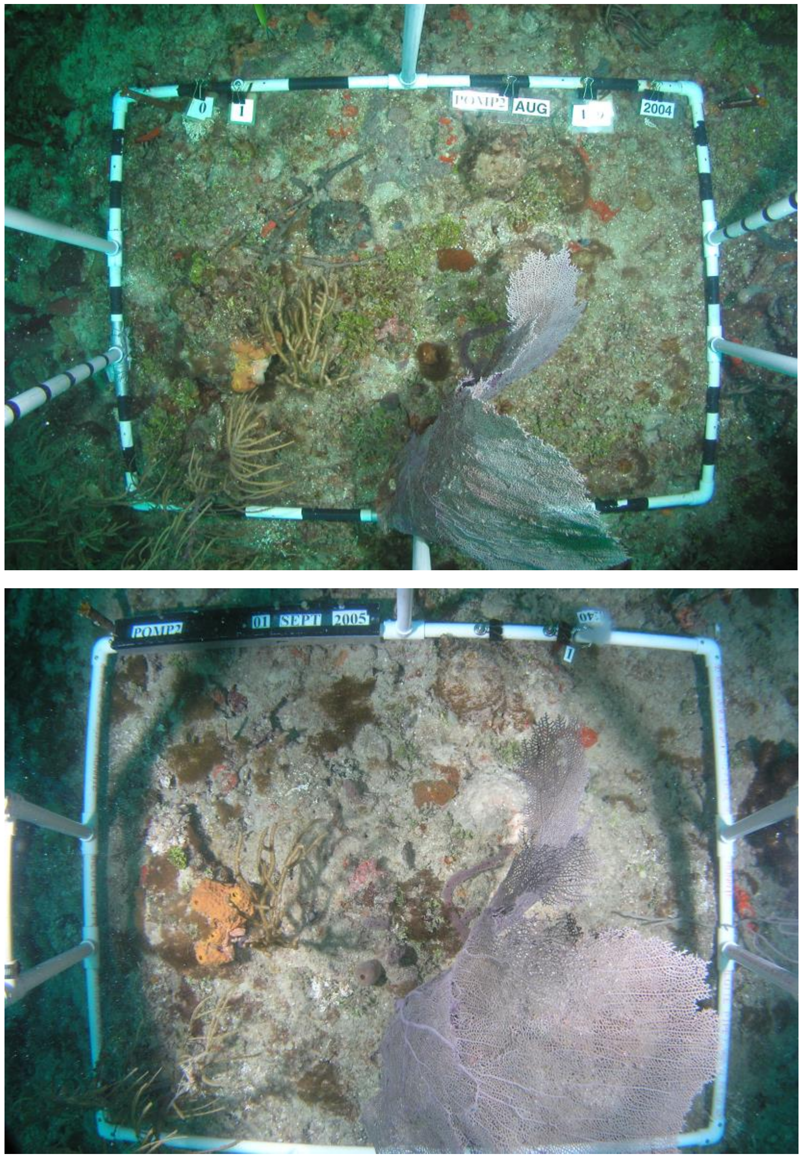


Figure 31: ***A:*** *Site POMP2 before (left) and after (right) Hurricane Katrina.*

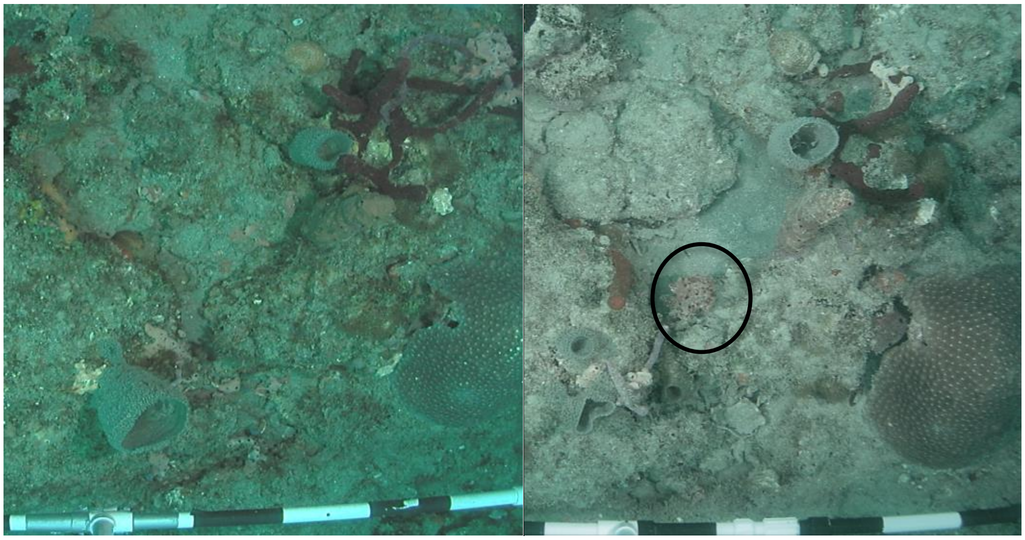


Figure 32: Site DB2 before (left) and after Hurricane Katrina and Wilma. Black circle shows recruitment of M. arbuscula *after the storms*.

4.1.3 Water Column Parameters and Latitude

The significant decreases in richness and abundance on the CPS from 2008-2010 and the increases on the RC from 2010-2011 are likely linked to a cold-water event in 2010. Lirman *et al.* (2011) reported that the optimum temperature for coral growth on the SEFRT is 26-27°C. However, temperatures beginning in January 2010 reached a record low, with several days below 16°C, which resulted in a significant decrease in soft and hard corals (Lirman *et al.*, 2011; Gilliam, 2012). Sponges appear to have a higher threshold for temperature variation (Duckworth *et al.*, 2012). Despite an initial decrease in abundance of several species from 2008 to 2010 at nearly all sites, which was significant on the CPS, abundance and richness of most species recovered by 2011, mainly at the northern sites such as, POMP1, POMP4, and DB3. However, whereas some southern sites exhibited no change in either abundance or richness, e.g., JUL2 and FTL6, others, e.g., FTL5, JUL1 and HH2, declined continuously in abundance. In addition, several of the northern LMR and LOR sites, e.g., HB2, HB3, and POMP3 experienced increases in abundance from 2008 to 2011 rather than decreases. However, as no species uniquely distinguished northern versus southern sites, the differences may just have resulted from more available space as corals declined (Lirman *et al.*, 2011).

Species richness did not decrease from south to north, contrary to the latitudinal gradient exhibited by many coral species along the SEFRT (Gilliam, 2012; Walker, 2012). This is likely due to location of sites on different reef types, with different substrate reliefs, depths, and different shore-related factors. A slight increase in abundance at higher latitudes on the middle and outer reefs is likely due to proximity to the Boca Raton and Broward/Pompano sewage outfalls (Banks *et al.*, 2008; Campbell *et al.*, 2015). Sponges thrive and exhibit higher abundance and richness in areas with increased dissolved organic matter (DOM), (de Goeij *et al.*, 2013; Pawlik *et al.*, 2018). A natural cycle between available nutrients and sponge growth, often referred to as the sponge loop, does occur between sponges, coral, and algae but is most obvious between sponges and algae (Figure 33) (de Goeij *et al.*, 2013). The sponge loop, and its effects on coral reef dynamics, is still not fully understood, but it plays a key role in the distribution of DOM and in the fluctuations between sponge and algal growth (Pawlik *et al.*, 2016; de Goeij *et al.*, 2017). The recent red tide outbreaks due to the release of nutrient-rich Lake Okeechobee freshwater may contribute to declines in sponge communities in the future. Continued observations of SEFRT sites and research on the sponge loop are necessary to understand how sponges might react to or recover from severe algal blooms in Broward County.

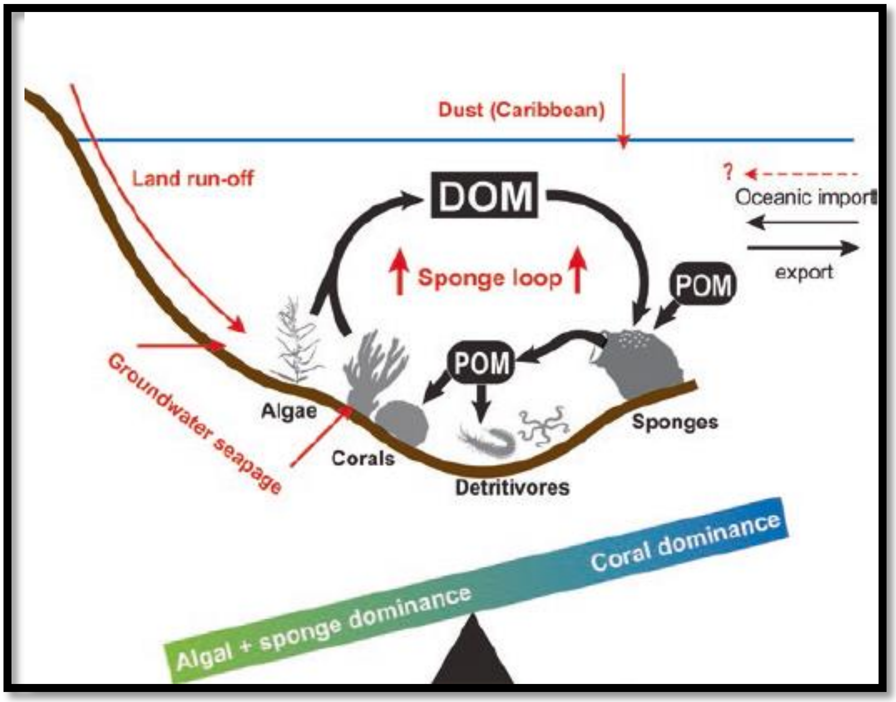


Figure 33: Example of the sponge loop (de Goeij et al., 2017).

As sponge assemblage composition exhibited significant changes at the study sites on the SEFRT from 2000 to 2015, hypothesis one is not rejected. The change in composition appears to have been associated with natural stressors rather than anthropogenic stressors, although beach-renourishment-associated burial likely caused limited and apparently temporary losses.

4.2 Hypothesis Two

Reef-building corals have been in decline since the 1980s, and it is important to establish the population dynamics of other common groups that offer structure and habitat on these reefs, and may replace stony corals in time (Hoegh-Guldberg *et al.*, 2007; Mumby and Steneck, 2008; Burke *et al.*, 2011; Stocker *et al.*, 2013; Maynard *et al.*, 2017; Bartlett *et al.*, 2018). In addition to macroalgae and soft corals, sponges are consistently dominant species (Bell *et al.*, 2017b). Although the once-yearly surveys did not allow any examination of possible seasonal variations in recruitment, the photographic data did provide interesting insights. The massive morphotype *X. muta* was more common on the outer reef, while the other four species (*I. stobilina, Ai. crassa, Am. compressa,* and *D. anchorata*) thrived on the middle reef. In addition, due to their slow growth rates, new recruits of the massive species were easy to monitor through time, while young *Am. compressa* and *D. anchorata* were hard to identify.

Aiolochroia crassa is a common, brightly colored, thick encrusting to massive tropical species (Villamizar *et al.*, 2014). It exhibited a slow, steady growth rate relative to the more rapidly growing *Am. compressa* and *D. anchorata.* This species colonized rapidly when space was available but often declined in abundance shortly after, as seen following the 2004-2005 hurricanes and the cold-water event in 2010-2011 (Figure 34). Area covered peaked in 2012, followed by a continuous decline in area and abundance. Perhaps this species was unable to compete with macroalgae and octocorals as they recovered from natural and anthropogenic events. However, *Ai. crassa* is chemically defended and rarely overgrown by other sponges (Engel and Pawlik, 2005; Loh and Pawlik, 2014). Therefore, factors contributing to its mortality remain unknown.

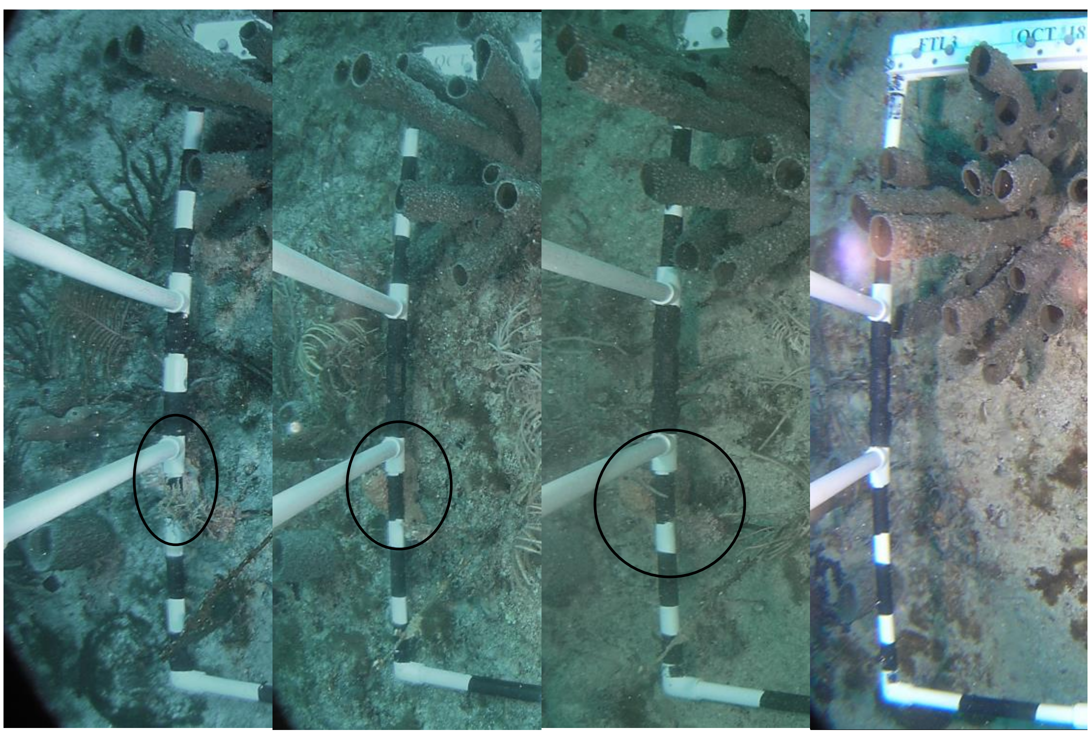


Figure 34: Time series of Ai. crassa *(left to right: 2008, 2010, 2011, 2012) before, during, and after the cold-water event in 2010. (No images were taken in 2009.)*

Amphimedon compressa was the most common branching species at study sites overall, and coverage was consistently high. As with other species declines, those of *Am. compressa* appeared be linked to hurricanes and cold-water events. However, images did not properly depict post-hurricane destruction, as half the sites were visited before Hurricane Wilma. Also, the combination of this species' small basal attachment and the vast sea of dead sponges, including many *Am. compressa*, washed ashore after Hurricane Irma (Figure 35) (Mercado and Yoshioka, 2009) suggest that damage to this species was far more extensive. In addition, lower observed mortality may have been due to fragmentation/high partial mortality and a high percentage of reattachment following disturbances (Wulff, 2013).

Figure 35: Dead sponges along JUL beach following Hurricane Irma. Arrows indicate some Am. compressa.

The population dynamics of *Desmapsamma anchorata* were inconsistent and exhibited a downward trend (Figures 28A, 29). It was most abundant on the LMR. Most individuals exhibited either a rope/runner morphotype along the bottom or encrusting on another organism such as *Callyspongia vaginalis* or *Aplysina cauliformis* (Figure 36). The encrusting morphotype was the most common but also yielded a short lifespan, as *D. anchorata* would either completely overgrow the organism, smothering its host or inflicting structural damage, leading to uprooting of the host (Figure 36). Similarly,Mclean *et al.* (2015) observed the weakening of gorgonian axes following *D. anchorata* attachment. While the rope/runner morphotype was able to survive for nearly five years, the species averaged a two-year lifespan. Peak abundance was seen in 2007 (65 y^{-1}) and was likely a response to the hurricanes in 2005 (Figure 28A). This species is often described as a weedy, rapid colonizer, and Wulff (2008); Flynn *et al.* (2016) both recorded it in high abundance following natural or anthropogenic events. In contrast, *D. anchorata* declined greatly in abundance from 2010 to 2013 as a result of the cold-water event mentioned above. This event caused a mass mortality of the hard coral *Acropora cervicornis* at several sites including FTL6, which caused the attached *D. anchorata* to perish (Lirman *et al.*, 2011; Gilliam, 2012). Octocoral and hard coral hosts require several years to recover, which may explain why there was a small increase in *D. anchorata* abundance between 2014 and 2015. However, further annual observations are needed to accurately determine if abundance is on an upward trend or not.

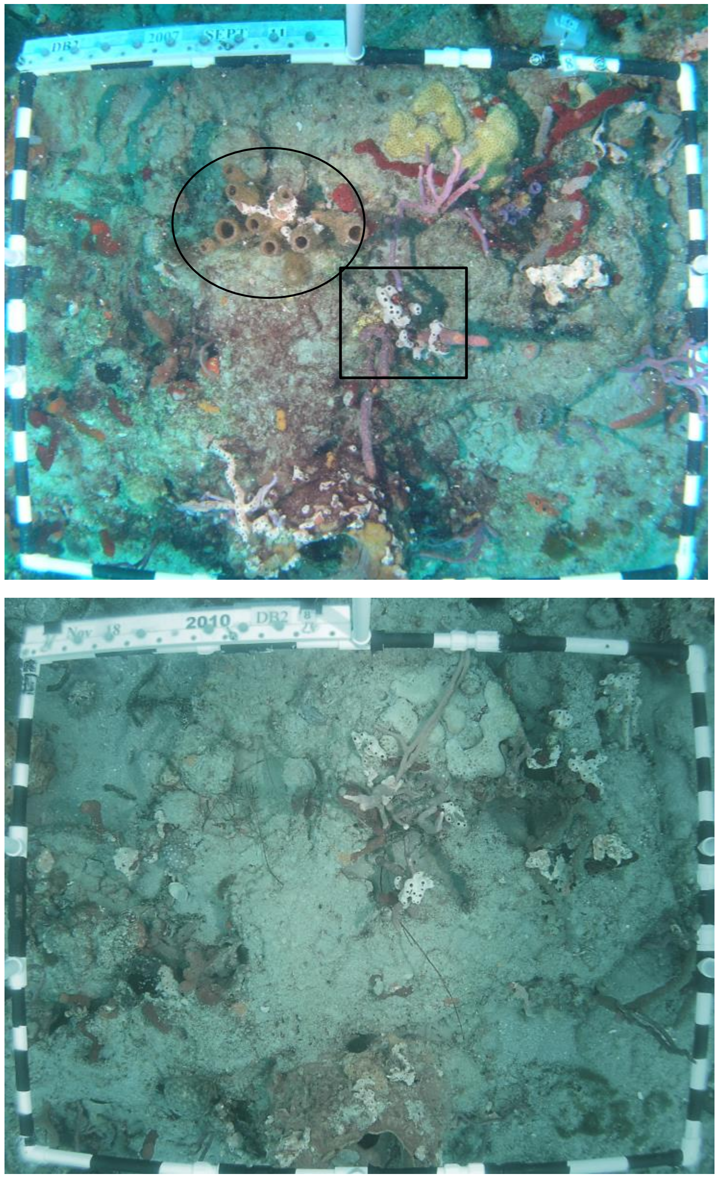


Figure 36: Site POMP2 in 2007 (left) and 2010 (right). Note interactions of D. anchorata *with* C. vaginalis *(circle) and* A. cauliformis *(box) and loss of the former in 2010.*

Ircinia strobilina is a massive, black, ball-shaped sponge that was found on all reef types. This species had higher fluctuations in coverage than other species (Figure 29D). Although the change was not enough to be significant, *I. strobilina* would increase in size for several years, e.g., at FTL2 by 40 cm^2 yr^{-1}, decrease for a year by 50 cm^2, and increase again the following year by 22 cm^2. The cause is unknown but may be due to timing of annual site visits relative to season. *Ircinia strobilina* exhibits seasonality and is often larger in the summer months, which also explains the loss of individuals between 2008-2010, when temperatures were at a record low (Leong and Pawlik, 2010; Lirman *et al.*, 2011).

Xestospongia muta, the giant barrel sponge, was included in this study, because it is the most commonly investigated local sponge due to its size, long lifespan, and importance as a reef habitat for many invertebrates and vertebrates (McMurray *et al.*, 2008). Although coverage increased continuously over time, total abundance at study sites exhibited a downward trend from 2007 to 2010. This decline may have been a delayed response to the hurricanes in 2004 and 2005, as lost individuals exhibited signs of distress before they died, e.g., bleaching and an orange/red discoloration consistent with sponge orange band disease (SOB) (Angermeier *et al.*, 2011; McMurray *et al.*, 2011). Given the importance of *X. muta* on reefs, any continued stress on this species, and the potential threat of SOB, could have serious consequences. These photo transects should, therefore, be continued. Despite this decline, *X. muta* populations were stable with steady recruitments. *Xestospongia muta* generally survived the entire length of the study, and the few losses were not the result of any one identifiable factor, e.g., temperature, disease or overgrowth. Mortality was higher in young *X. muta*, implying an increased chance of survival with age, supporting McMurray *et al.* (2010), who observed no mortality of recruits that reached five years old. The results of this study concur with McMurray (2008; 2010; 2011; 2015), who has extensively documented the population dynamics of *X. muta* in the Florida Keys.

5. Conclusion

From 2000 to 2015, sponge assemblages off Broward County have seen significant changes in species richness and abundance while maintaining high-diversity communities. Total sponge abundance significantly increased from 2000 to 2015. However, individual reef types and sites exhibited spatial and temporal variations. Spatial trends depended on reef type and depth. Temporal trends were likely related to the sponge loop and exaggerated by natural and anthropogenic events (Figure 37).

Unfortunately, due to the timing of the annual surveys, hurricanes and beach renourishments, we cannot disentangle the effects of compounding variables on reef sponges. In addition, the lack of funding and annual surveys in 2009 made it difficult to establish if the cold-water event in early 2010 contributed to a decline in abundance during 2010 or if another unknown factor was responsible. However, as natural and anthropogenic events are predicted to increase in abundance and intensity, it is important to continue to monitor these sites. In addition, because macroalgae are important competitors for space with sponges, further analyses of the interactions of these two groups are encouraged.

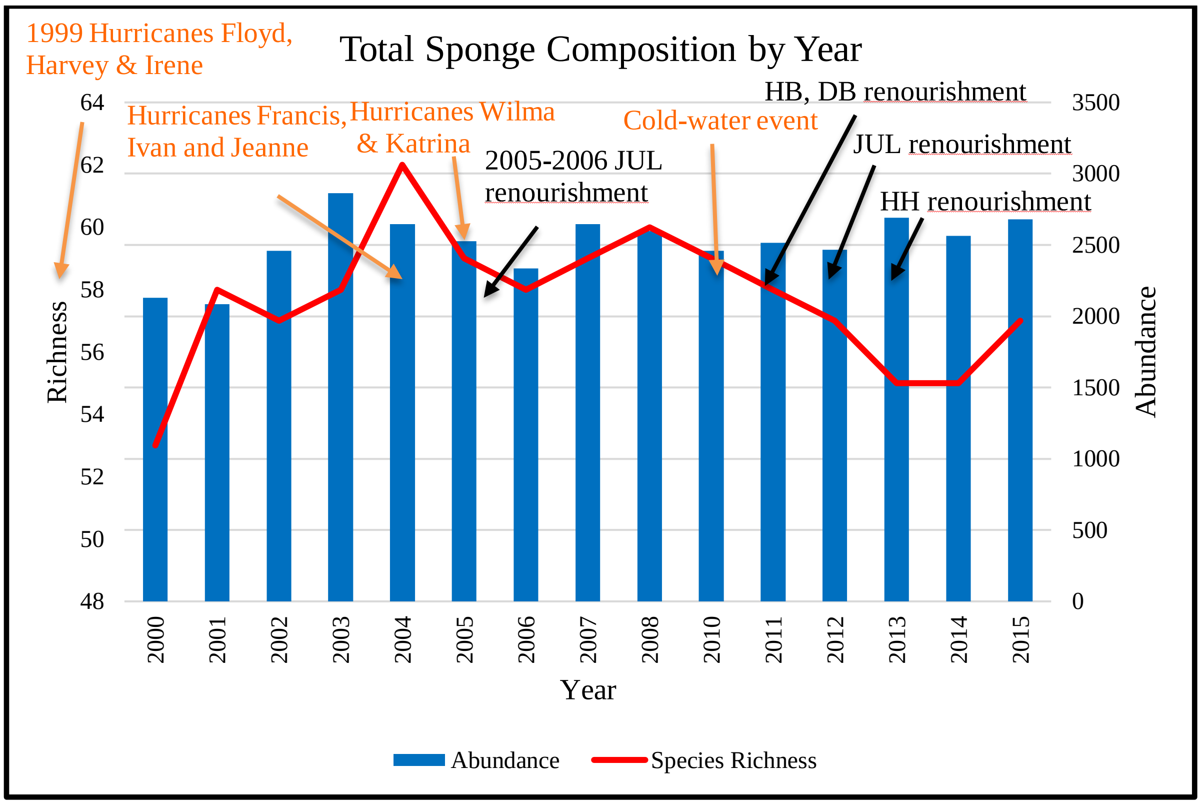


Figure 37:Total Sponge composition, natural (orange arrows) and anthropogenic (black arrows) events between 2000 and 2015.

The five species (*Ai. crassa, Am. compressa, D. anchorata, I. strobilina,* and *X. muta*) examined over time provided insights into the population dynamics of common sponges of different morphotypes. Adding *in situ* environmental parameters to images is highly suggested for future studies, and measuring sponge volume would provide more accurate information, because many sponge species grow vertically. Biannual visits would also give a more accurate picture of species-level responses to natural and anthropogenic events. Sponges are important invertebrates on coral reef systems and, although not currently as threatened as hard corals, they should not be ignored.

REFERENCES

(2018). *Beach Renourishment*. Broward County Government. http://www.broward.org/BeachRenourishment/Pages/Partners.aspx.

Anderson, M.J., and Santana, G. J. (2015). Measures of precision for dissimilarity - based multivariate analysis of ecological communities. *Ecology Letters* 18(1)**,** 66-73. doi: 10.1111/ele.12385.

Angermeier, H., Kamke, J., Abdelmohsen, U.R., Krohne, G., Pawlik, J.R., Lindquist, N.L., et al. (2011). The pathology of sponge orange band disease affecting the Caribbean barrel sponge *Xestospongia muta*. *FEMS Microbiology Ecology* 75(2)**,** 218-230. doi: 10.1111/j.1574-6941.2010.01001.x.

Banks, K.W., Riegl, B.M., Richards, V.P., Walker, B.K., Helmle, K.P., Jordan, L.K., et al. (2008). The reef tract of continental southeast Florida (Miami-Dade, Broward and Palm Beach counties, USA). *Coral Reefs of the USA***,** 175-220.

Bartlett, L.A., Brinkhuis, V.I., Ruzicka, R.R., Colella, M.A., Lunz, K.S., Leone, E.H., et al. (2018). "Dynamics of stony coral and octocoral juvenile assemblages following disturbance on patch reefs of the florida reef tract,"In *Corals in a Changing World*. eds. Beltran & Camacho. InTech. 100-120. doi: 10.5772/intechopen.71606.

Bell, J.J. (2007). Contrasting patterns of species and functional composition of coral reef sponge assemblages. *Marine Ecology Progress Series* 339**,** 73-81. 0171-8630.

Bell, J.J. (2008). Sponges as agents of biological disturbance. *Marine Ecology Progress Series* 368**,** 127-135.

Bell, J.J., and Barnes, D.K.A. (2003). Effect of disturbance on assemblages: an example using porifera. *Biological Bulletin* 205(2)**,** 144-159. doi: 137.52.20.243.

Bell, J.J., Biggerstaff, A., Bates, T., Bennett, H., Marlow, J., McGrath, E., et al. (2017a). Sponge monitoring: Moving beyond diversity and abundance measures. *Ecological Indicators* 78**,** 470-488. 1470-160X.

Bell, J.J., Davy, S.K., Jones, T., Taylor, M.W., and Webster, N.S. (2013). Could some coral reefs become sponge reefs as our climate changes? *Global Change Biology* 19(9)**,** 2613-2624. doi: 10.1111/gcb.12212.

Bell, J.J., McGrath, E., Biggerstaff, A., Bates, T., Bennett, H., Marlow, J., et al. (2015). Sediment impacts on marine sponges. *Marine pollution bulletin* 94(1-2)**,** 5-13. 0025-326X.

Bell, J.J., Shaffer, M., Bennett, H., McGrath, E., Mortimer, C., Rovellini, A., et al. (2017b). "Impacts of short-term large-scale climatic variation on sponge assemblages,"In *Climate Change, Ocean Acidification and Sponges*. eds. Bell & Carballo. Springer. 143-177. doi: 10.1007/978-3-319-59008-0_6.

Bouchet, P. (2006). "The magnitude of marine biodiversity,"In *The Exploration of Marine Biodiversity: Scientific and Technological Challenges*. ed. Duarte. Fundación BBVA. 978-84-96515-27-7.

Bretz, F., Westfall, P., and Hothorn, T. (2016). *Multiple comparisons using R.* Chapman and Hall/CRC.

Burke, L., Reytar, K., Spalding, M., and Perry, A. (2011). *Reefs at risk revisited.* Washington DC: World Resources Institute.

Bush, S.J. (2012). *Post-injury recovery, reattachment, survival and growth of the giant barrel sponge, Xestospongia muta, offshore Southeast Florida.* M.S. Thesis, Nova Southeastern University. http://nsuworks.nova.edu/occ_stuetd/193. .

Campbell, A.M., Fleisher, J., Sinigalliano, C., White, J.R., and Lopez, J.V. (2015). Dynamics of marine bacterial community diversity of the coastal waters of the reefs, inlets, and wastewater outfalls of southeast Florida. *MicrobiologyOpen* 4(3)**,** 390-408. doi: 10.1002/mbo3.245.

Carballo, J.L., Bautista, E., Nava, H., Cruz-Barraza, J.A., and Chávez, J.A. (2013). Boring sponges, an increasing threat for coral reefs affected by bleaching events. *Ecology and Evolution* 3(4)**,** 872-886. doi: 10.1002/ece3.452.

Carballo, J.L., Vega, C., Cruz-Barraza, J.A., Yanez, B., Nava, H., Avila, E., et al. (2008). Short and long term patterns of sponge diversity on a rocky tropical coast: evidence of large scale structuring factors. *Marine Ecology* 29(2)**,** 216-236. doi: https://doi.org/10.1111/j.1439-0485.2008.00228.x.

Carpenter, K.E., Abrar, M., Aeby, G., Aronson, R.B., Banks, S., Bruckner, A., et al. (2008). One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* 321(5888)**,** 560-563. 0036-8075.

Cerrano, C. (2004). Lagoon sponges from Carrie Bow Cay (Belize): ecological benefits of selective sediment incorporation. *BMIB-Bollettino dei Musei e degli Istituti Biologici* 68. 2611-5786.

Cesar, H., Burke L., and L, P.-S. (2003). "The Economics of Worldwide Coral Reef Degradation". Cesar Environmental Economics Consulting (CEEC). https://www.wwf.or.jp/activities/lib/pdf_marine/coral-reef/cesardegradationreport100203.pdf.

Clarke, K.R., and Warwick, R.M. (2014). *Change in Marine Communities: an Approach to Statistical Analysis and Interpretation.* Plymouth: PRIMER-E. 260

de Goeij, J.M., Lesser, M.P., and Pawlik, J.R. (2017). "Nutrient fluxes and ecological functions of coral reef sponges in a changing ocean,"In *Climate Change, Ocean Acidification and Sponges*. eds. Bell & Carballo. Springer. 373-410. doi: 10.1007/978-3-319-59008-0_8.

de Goeij, J.M., van Oevelen, D., Vermeij, M.J.A., Osinga, R., Middelburg, J.J., de Goeij, A.F.P.M., et al. (2013). Surviving in a marine desert: The Sponge Loop retains resources within coral reefs. *Science* 342(6154)**,** 108-110. doi: 10.1126/science.1241981.

De Voogd, N.J., and Cleary, D.F. (2008). An analysis of sponge diversity and distribution at three taxonomic levels in the Thousand Islands/Jakarta Bay reef complex, West‐Java, Indonesia. *Marine Ecology* 29(2)**,** 205-215. 1439-0485.

DeJong, T. (1975). A comparison of three diversity indices based on their components of richness and evenness. *Oikos***,** 222-227. 0030-1299.

Diaz, C.M., and Rutzler, K. (2001). Sponges: an essential component of Caribbean coral reefs. *Bulletin of Marine Science* 69(2)**,** 535-546.

Dodge, R.E., Goldberg, W., Hess, S.C., and Messing, C. (1991a). "Preconstruction Report: Biological Monitoring of the Hollywood-Hallandale Beach Renourishment: 1991". Broward County Board of County Commissioners Erosion Prevention District of the Office of Natural Resource Protection.

Dodge, R.E., Hess, S.C., and Messing, C. (1991b). "Final Report: Biological Monitoring of the John U. Lloyd Beach Renourishment: 1989". Nova Southeastern University Oceanographic Center and Environmental Resources Management South, Inc.

Dodge, R.E., Hess, S.C., Messing, C., and Kelly, G. (1989). ""Phase I- Preconstruction Progress Report for Biological Monitoring of the John U. Lloyd Beach Renourishment"". https://nsuworks.nova.edu/occ_facreports/27.

Duckworth, A.R., West, L., Vansach, T., Stubler, A., and Hardt, M. (2012). Effects of water temperature and pH on growth and metabolite biosynthesis of coral reef sponges. *Marine Ecology Progress Series* 462**,** 67-77. 0171-8630.

Engel, S., and Pawlik, J.R. (2005). Interactions among Florida sponges. I. Reef habitats. *Marine Ecology Progress Series* 303**,** 133-144. doi: 10.3354/meps303133.

Fisher, L., Banks, K., Gilliam, D.S., Dodge, R.E., Stout, D., Vargas-Ángel, B., et al. (Year). "Real-time coral stress observations before, during, and after beach nourishment dredging offshore SE Florida", in: *Proceedings of the 11th International Coral Reef Symposium* https://nsuworks.nova.edu/occ_facpresentations/42.

Florida Department of Environmental Protection, F. (2016). *Florida's Coral Reef Protection Act*. https://floridadep.gov/sites/default/files/coral-reef-protection-052016.pdf.

Flynn, K., Griffin, S.P., Spathias, H., Hernández-Delgado, E.A., Bejarano, I., Medina-Muñiz, J.L., et al. (2016). 2016 Monitoring Report for Emergency Restoration following the T/V Port Stewart grounding in 2009 Yabucoa, Puerto Rico. For: NOAA Restoration Center, St. Petersburg, FL PR Department of Natural and Environmental Resources, San Juan, PR and Polaris Applied Science, Inc. https://casedocuments.darrp.noaa.gov/southeast/port_stewart/pdf/2016_Port_Stewart_Monitoring_Report.pdf.

Freeman, C.J., Daniel F. Gleason, Rob Ruzicka, Rob W.M. Van Soest, Harvey, A.W., and McFall, G. (2007). "A biogeographic comparison of sponge fauna from Gray's Reef National Marine Sanctuary and other hard-bottom reefs of coastal Georgia, U.S.A.,"In *Porifera research; biodiversity,innovation and sustainability*. Serie Livros. 319-325. http://www2.ib.usp.br/~mcust/7thISS/09-book/pdf/Freeman%20et%20al%20-%20Biogeographic%20comparison%20of%20sponge%20fauna.pdf.

Gilliam, D.S. (2012). "Southeast Florida Coral Reef Evaluation and Monitoring Project 2011 Year 9 Final Report". Florida DEP Report #RM085. https://nsuworks.nova.edu/cgi/viewcontent.cgi?referer=https://www.google.com/&httpsredir=1&article=1075&context=occ_facreports.

Halperin, A. (2014). *Distribution, growth, and impact of the coral-excavating sponge, Cliona delitrix, on the stony coral communities offshore Southeast Florida.* M.S. Thesis, Nova Southeastern University. http://nsuworks.nova.edu/occ_stuetd/26.

Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., et al. (2007). Coral reefs under rapid climate change and ocean acidification. 318(5857)**,** 1737-1742. 0036-8075.

Holmes, K. (1997). "Eutrophication and its effect on bioeroding sponge communities", in: *Proceedings of the 8th International Coral Reef Symposium*, eds. Lessios & I.G. (1997, 1411-1416.

Hooper, J.N., Van Soest, R.W., and Debrenne, F. (2002). "Phylum Porifera Grant, 1836,"In *Systema Porifera: A Guide to the Classification of Sponges*. eds. Hooper & Van Soest. Springer. 9-13. https://www.researchgate.net/profile/John_Hooper/publication/233979436_Phylum_Porifera_Grant_1826/links/0fcfd50f81f9dedeae000000.pdf.

Hothorn, T., Bretz, F., Westfall, P., Heiberger, R.M., Schuetzenmeister, A., Scheibe, S., et al. (2017). Package 'multcomp'. *Obtenido de http://cran. statsfu. ca/web/packages/multcomp/multcomp*.

Hughes, T.P. (1994). Catastrophes, phase shifts and large-scale degradation of a Caribbean coral reef. *Science* 265(5178)**,** 1547-1551. doi: 10.1126/science.265.5178.1547.

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., et al. (2003). Climate change, human impacts, and the resilience of coral reefs. 301(5635)**,** 929-933. 0036-8075.

Humann, P. (2002). *Reef Coral Identification: Florida, Caribbean, Bahamas.*: New World Publications.

IPCC (2013). Stocker, T., Qin, D., Plattner, G., Tignor, M., Allen, S., Boschung, J., et al. (2013). *The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change,* Cambridge Univ. Press, Cambridge, UK, and New York.1535 pp. https://www.ipcc.ch/site/assets/uploads/2017/09/WG1AR5_Frontmatter_FINAL.pdf.

Jaap, W.C. (1984). "Ecology of the South Florida coral reefs: a community profile". U.S. Fish and Wildlife Service, FWS/OBS-82/08. Minerals Management Service MMS 84-0038. https://www.boem.gov/ESPIS/3/3860.pdf.

Kohler, K.E.a.G., S.M. (2006). Coral Point Count with Excel extensions(CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers and Geosciences* 32(9)**,** 1259-1269.

Kruskal, J.B., and Wish, M. (1978). *Multidimensional Scaling.* SAGE Publications.

Laird, N.M., and Ware, J.H.J.B. (1982). Random-effects models for longitudinal data. 38(4)**,** 963-974. 0006-341X.

Leong, W., and Pawlik, J.R. (2010). Evidence of a resource trade-off between growth and chemical defenses among Caribbean coral reef sponges. *Marine Ecology Progress Series* 406**,** 71-78. 0171-8630.

Lessios, H.A. (1988). Mass mortality of *Diadema antillarum* in the Caribbean: What have we learned? *Annual Review of Ecology and Systematics* 19**,** 371-393.

Lirman, D., Schopmeyer, S., Manzello, D., Gramer, L.J., Precht, W.F., Muller-Karger, F., et al. (2011). Severe 2010 cold-water event caused unprecedented mortality to corals of the Florida reef tract and reversed previous survivorship patterns. *PLoS one* 6(8)**,** e23047. 1932-6203.

Loh, T.-L., and Pawlik, J.R. (2014). Chemical defenses and resource trade-offs structure sponge communities on Caribbean coral reefs. *Proceedings of the National Academy of Sciences* 111(11)**,** 4151-4156. doi: 10.1073/pnas.1321626111.

Maldonado, M., Aguilar, R., Bannister, R.J., Bell, J.J., Conway, K.W., Dayton, P.K., et al. (2015). "Sponge Grounds as Key Marine Habitats: A Synthetic Review of Types, Structure, Functional Roles, and Conservation Concerns,"In *Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots*. eds. Rossi, Bramanti, Gori & Orejas Saco del Valle. Springer International Publishing. 1-39. doi: 10.1007/978-3-319-17001-5_24-1.

Maliao, R.J., Turingan, R.G., and Lin, J. (2008). Phase-shift in coral reef communities in the Florida Keys National Marine Sanctuary (FKNMS), USA. *Marine Biology* 154**,** 841-853. doi: 10.1007/s00227-008-0977-0.

Malmstadt, J., Scheitlin, K., and Elsner, J. (2009). Florida Hurricanes and Damage Costs. *Southeastern Geographer* 49(2)**,** 108-131. 0038-366X.

Maynard, J., Byrne, J., Kerrigan, K., Tracey, D., Bohnsack, K., Pagan, F., et al. (2017). "Coral reef resilience to climate change in the Florida Reef Tract". Florida Department of Environmental Protection, Coral Reef Conservation Program. ftp://ftp.library.noaa.gov/noaa_documents.lib/CoRIS/CRCP_198_Maynard_2017.pdf.

Mclean, E.L., Rutzler, K., and Pooler, P.S. (2015). Competing for space: Factors that lead to sponge overgrowth when interacting with octocoral. *Journal of Marine Science* 5**,** 64-80. doi: http://dx.doi.org/10.4236/ojms.2015.51007.

McMurray, S., Blum, J.E., and Pawlik, J.R. (2008). Redwood of the reef: growth and age of the giant barrel sponge *Xestospongia muta* in the Florida Keys. *Marine Biology* 155(2)**,** 159-171. 0025-3162.

McMurray, S.E., Blum, J.E., Leichter, J.J., and Pawlik, J.R. (2011). Bleaching of the giant barrel sponge *Xestospongia muta* in the Florida Keys. *Limnology and Oceanography* 56(6)**,** 2243-2250. 0024-3590.

McMurray, S.E., Finelli, C.M., and Pawlik, J.R. (2015). Population dynamics of giant barrel sponges on Florida coral reefs. *Journal of Experimental Marine Biology and Ecology* 473**,** 73-80. 0022-0981.

McMurray, S.E., Henkel, T.P., and Pawlik, J.R. (2010). Demographics of increasing populations of the giant barrel sponge *Xestospongia muta* in the Florida Keys. *Ecology* 91(2)**,** 560-570. doi: https://www.jstor.org/stable/25661081.

McMurray, S.E., Stubler, A.D., Erwin, P.M., Finelli, C.M., and Pawlik, J.R. (2018). A test of the sponge-loop hypothesis for emergent Caribbean reef sponges. *Marine Ecology Progress Series* 588**,** 1-14. 0171-8630.

Mercado, M., and Yoshioka, P.M. (2009). Relationships between water motion and size-specific survivorship and growth of the demosponge *Amphimedon compressa*. *Journal of Experimental Marine Biology and Ecology* 375**,** 51-56. doi: https://doi.org/10.1016/j.jembe.2009.05.003.

Meurer, B.C., Lages, N.S., Pereira, O.A., Palhano, S., and Magalhaes, G.M. (2010). First record of native species of sponge overgrowing invasive corals *Tubastraea coccinea* and *Tubastraea tagusensis* in Brazil. *Marine Biodiversity Records* 3. doi: 10.1017/S1755267210000527.

Mumby, P.J., and Steneck, R.S. (2008). Coral Reef Management and Conservation in Light of Rapidly Evolving Ecological Paradigms. *Trends in Ecology and Evolution* 23(10)**,** 555-563. doi: 10.1016/j.tree.2008.06.011.

Murray, L. (2010). *Biostatistical design and analysis using R, a practical guide.* UK: Wiley-Blackwell.

NOAA (2016). *Atlantic Hurricane Season Archives*. Florida: National Hurricane Center. https://www.nhc.noaa.gov/data/tcr/index.php?season=2016&basin=atl.

OAI. (2011). "Broward County Shore Protection Project- Segment III Broward County, FL, 5- Year Post-Contruction Physical Monitoring Report". Engineering report prepared for Broward County Board of County Commissioners, Olsen Associates, Inc. Jacksonville, FL, December 2011.

Pawlik, J.R., Burkepile, D.E., and Thurber, R.V. (2016). A vicious circle? Altered carbon and nutrient cycling may explain the low resilience of Caribbean coral reefs. *Bioscience* 66(6)**,** 470-476. 0006-3568.

Pawlik, J.R., Loh, T., and McMurray, S.E. (2018). A review of bottom-up vs. top-down control of sponges on Caribbean fore-reefs: what's old, what's new, and future directions. *PeerJ* 6**,** e4343. doi: https://doi.org/10.7717/peerj.4343.

Pawlik, J.R., T. Henkel, McMurray, S.E., Lopez-Legentil, S., Loh, T., and Rohde, S. (2008). Patterns of sponge recruitment and growth on a shipwreck corroborate chemical defense resource trade-off. *Marine Ecology Progress Series* 368**,** 137-143. doi: 10.3354/meps07615.

Peddycoart, M.R. (2010). *Variations in composition, abundance and cover of reef tract sponge assemblages in Broward County, Florida, 2002-2006.* M.S. Thesis, Nova Southeastern University. http://nsuworks.nova.edu/occ_stuetd/210.

Pineda, M.-C., Strehlow, B., Sternel, M., Duckworth, A., Jones, R., and Webster, N.S. (2017). Effects of suspended sediments on The sponge holobiont With implications for dredging management. *Scientific Reports* 7(1)**,** 4925. doi: 10.1038/s41598-017-05241-z.

Pinheiro, J., Bates, D., DebRoy, S., and Sarkar, D. (2014). R Core Team (2014) nlme: linear and nonlinear mixed effects models. R package version 3.1-117. *Available at h ttp://CRAN. R-project. org/package= nlme*.

Plaisance, L., Caley, J.M., Brainard, R.E., and Knowlton, N. (2011). The diversity of coral reefs: what are we missing? *PLoS One* 6(10)**,** e25026. doi: https://doi.org/10.1371/journal.pone.0025026.

Powell, A., Smith, D.J., Hepburn, L.J., Jones, T., Berman, J., Jompa, J., et al. (2014). Reduced diversity and high sponge abundance on a sedimented Indo-Pacific Reef system: implications for future changes in environmental quality. *PLoS One* 9(1)**,** e85253. doi: 10.1371/journal.pone.0085253.

Powell, M.D., and Houston, S.H. (1996). Hurricane Andrew's landfall in south Florida. Part II: Surface wind fields and potential real-time applications. *Weather and Forecasting* 11(3)**,** 329-349. 1520-0434.

Precht, W.F., and Miller, S.L. (2007). "Ecological shifts along the Florida Reef Tract: the past is a key to the future,"In *Geological Approaches to Coral Reef Ecology*. ed. Aronson. Springer. 237-312. http://people.uncw.edu/millers/documents/precht%20and%20miller%20ch.pdf.

Reiswig, H.M. (1974). Water transport, respiration and energetics of three tropical marine sponges. *Journal of Experimental Marine Biology and Ecology* 14(3)**,** 231-249. 0022-0981.

Rützler, K., and I.G., M. (1982). The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize, I: Structure and Communities. *Smithsonian Contributions to the Marine Sciences* 12**,** 539. doi: 10.5479/si.01960768.12.539.

Sathe, M.P. (2008). *Factors influencing Southeast Florida Coral reef community composition.* M.S Thesis, Nova Southeastern University Oceanographic Center. https://nsuworks.nova.edu/occ_facpresentations/43?utm_source=nsuworks.nova.edu%2Focc_facpresentations%2F43&utm_medium=PDF&utm_campaign=PDFCoverPages.

Small, A.M., Adey, W.H., and Spoon, D. (1998). Are current estimates of coral reef biodiversity too low? The view through the window of a microcosm. *Atoll Research Bulletin* 450**,** 20. 0077-5630.

Somerfield, P., Jaap, W., Clarke, K., Callahan, M., Hackett, K., Porter, J., et al. (2008). Changes in coral reef communities among the Florida Keys, 1996–2003. *Coral Reefs* 27(4)**,** 951-965. 0722-4028.

Spalding, M.D., Ravilious, C., Green, E.P. (2001). *World Atlas of Coral Reefs.* Berkeley California: University of California Press.

Thanner, S. (2004). *Comparison of the benthic assemblages on three types of artificial reef modules deployed in august of 1991.* Marine Biology, Nova Southeastern University. http://nsuworks.nova.edu/occ_stuetd/104

Van Soest, R., Boury-Esnault, N., Vacelet, J., Dohrmann, M., Erpenbeck, D., De Voogd, N.J., et al. (2012). Global diversity of sponges (Porifera). *PLoS One* 7(4)**,** e35105. doi: https://doi.org/10.1371/journal.pone.0035105.

Villamizar, E., Díaz, M.C., Rützler, K., and De Nóbrega, R. (2014). Biodiversity, ecological structure, and change in the sponge community of different geomorphological zones of the barrier fore reef at C arrie B ow C ay, B elize. *Marine Ecology* 35(4)**,** 425-435. 0173-9565.

Walker, B.K. (2012). Spatial analyses of benthic habitats to define coral reef ecosystem regions and potential biogeographic boundaries along a latitudinal gradient. *PLoS One* 7(1)**,** e30466. doi: 10.1371/journal.pone.0030466.

Walker, B.K., Riegl, B.M., and Dodge, R.E. (2008). Mapping coral reef habitats in southeast Florida using a combined technique approach. *Journal of Coastal Research* 24(5)**,** 1138-1150. doi: https://doi.org/10.2112/06-0809.1.

Wickham, H. (2016). *ggplot:Elegant Graphics for Data Analysis.* New York: Springer-Verlag.

Wilkinson, C., Souter, D. (2008). *Status of Caribbean coral reefs after bleaching and hurricanes in 2005.* Global Coral Reef Monitoring Network, and Reef, and Rainforest Reseach Centre, Townsville. 152 pp.

Wulff, J.L. (2006). Rapid diversity and abundance decline in a Caribbean coral reef sponge community. *Biological Conservation* 127(2)**,** 167-176. doi: https://doi.org/10.1016/j.biocon.2005.08.007.

Wulff, J.L. (2008). Life-history differences among coral reef sponges promote mutualism or exploitation of mutualism by influencing partner fidelity feedback. *The American Natualist* 171(5)**,** 597-609. doi: https://www.jstor.org/stable/10.1086/587067.

Wulff, J.L. (2013). Recovery of sponges after extreme mortality events: morphological and taxonomic patterns in regeneration versus recruitment. *Integrative and comparative biology* 53(3)**,** 512-523. doi: https://doi.org/10.1093/icb/ict059.

Zea, S., Henkel, T.P., and Pawlik, J.R. (2014). *The Sponge Guide:a picture guide to Caribbean sponges.* 3rd Edition. www.spongeguide.org.

APPENDICES

Significance is highlighted in yellow for all reef habitats, sites, and changes in area. Green marks significance of five-year intervals.

Appendix 1

PAIRWISE COMPARISONS of Broward County Sponge Assemblages from 2000 to 2015. Yellow highlight marks annual significance and green marks significance of five-year intervals.

Resemblance worksheet
Name: Resem5
Data type: Similarity
Selection: All
Transform: Fourth root
Resemblance: S17 Bray-Curtis similarity (+d)
Group factor: Year
Number of permutations: 9999
Number of groups: 15
Number of samples: 4037
DEVIATIONS FROM CENTROID
F: 2.8271 df1: 14 df2: 4022
P(perm): 0.0068

Year	t	P(Perm)
(2000,2001)	0.8307	0.4325
(2000,2002)	2.082	0.0471
(2000,2003)	4.2628	0.0001
(2000,2004)	4.513	0.0001
(2000,2005)	3.0509	0.0048
(2000,2006)	3.0789	0.0039
(2000,2007)	3.5385	0.0008
(2000,2008)	2.8012	0.0099
(2000,2010)	2.3551	0.0248
(2000,2011)	2.4501	0.0187
(2000,2012)	2.5942	0.0148
(2000,2013)	1.8479	0.0853
(2000,2014)	2.0402	0.0547
(2000,2015)	2.677	0.0104
(2001,2002)	1.324	0.2242
(2001,2003)	3.5135	0.0018
(2001,2004)	3.7446	0.0005
(2001,2005)	2.2842	0.0327
(2001,2006)	2.2647	0.0305
(2001,2007)	2.7618	0.0113
(2001,2008)	1.9944	0.0655
(2001,2010)	1.4568	0.1738
(2001,2011)	1.5803	0.1387
(2001,2012)	1.7575	0.1008
(2001,2013)	1.0477	0.3264
(2001,2014)	1.2366	0.2563
(2001,2015)	1.8961	0.0774
(2002,2003)	2.0855	0.0675
(2002,2004)	2.273	0.0459
(2002,2005)	0.88824	0.437
(2002,2006)	0.79654	0.4844
(2002,2007)	1.3248	0.2481

(2002,2008)	0.55313	0.6427
(2002,2010)	0.078053	0.9488
(2002,2011)	0.075282	0.9475
(2002,2012)	0.28715	0.7997
(2002,2013)	0.32591	0.7793
(2002,2014)	0.14979	0.9011
(2002,2015)	0.50159	0.6709
(2003,2004)	0.15318	0.8945
(2003,2005)	1.2409	0.2739
(2003,2006)	1.4145	0.2145
(2003,2007)	0.81902	0.4723
(2003,2008)	1.6466	0.1471
(2003,2010)	2.4156	0.0333
(2003,2011)	2.2224	0.0504
(2003,2012)	1.9609	0.0884
(2003,2013)	2.517	0.0304
(2003,2014)	2.3272	0.0448
(2003,2015)	1.638	0.1628
(2004,2005)	1.416	0.2181
(2004,2006)	1.5996	0.1611
(2004,2007)	0.98853	0.3839
(2004,2008)	1.8348	0.1143
(2004,2010)	2.633	0.0212
(2004,2011)	2.4313	0.0329
(2004,2012)	2.1596	0.0578
(2004,2013)	2.7207	0.0168
(2004,2014)	2.5274	0.0265
(2004,2015)	1.8214	0.115
(2005,2006)	0.13175	0.9092
(2005,2007)	0.43808	0.6979
(2005,2008)	0.37444	0.74
(2005,2010)	1.0821	0.3439
(2005,2011)	0.90714	0.4377

(2005,2012)	0.66804	0.5636
(2005,2013)	1.2658	0.2731
(2005,2014)	1.0818	0.351
(2005,2015)	0.40066	0.7317
(2006,2007)	0.58792	0.6107
(2006,2008)	0.25374	0.8272
(2006,2010)	0.99008	0.3796
(2006,2011)	0.80704	0.4776
(2006,2012)	0.55817	0.629
(2006,2013)	1.1852	0.3014
(2006,2014)	0.99488	0.3805
(2006,2015)	0.28468	0.8119
(2007,2008)	0.83027	0.479
(2007,2010)	1.5756	0.1711
(2007,2011)	1.3896	0.2375
(2007,2012)	1.137	0.3342
(2007,2013)	1.7278	0.1466
(2007,2014)	1.5399	0.1903
(2007,2015)	0.84421	0.4739
(2008,2010)	0.71235	0.5346

(2008,2011)	0.53642	0.652
(2008,2012)	0.29612	0.8029
(2008,2013)	0.9268	0.4369
(2008,2014)	0.73856	0.5239
(2008,2015)	0.037904	0.9752
(2010,2011)	0.17501	0.88
(2010,2012)	0.41429	0.7196
(2010,2013)	0.28993	0.8032
(2010,2014)	0.089222	0.939
(2010,2015)	0.65039	0.5739
(2011,2012)	0.23925	0.8434
(2011,2013)	0.44326	0.702
(2011,2014)	0.24683	0.8296
(2011,2015)	0.48079	0.6789
(2012,2013)	0.65637	0.566
(2012,2014)	0.46455	0.691
(2012,2015)	0.24873	0.8305
(2013,2014)	0.18439	0.8715
(2013,2015)	0.86255	0.4671
(2014,2015)	0.6797	0.5664

MEANS AND STANDARD ERRORS

Group	Size	Average	SE
2000	253	45.821	0.34145
2001	253	45.405	0.36607
2002	253	44.624	0.46225
2003	275	43.198	0.49969
2004	275	43.091	0.48785
2005	275	44.043	0.46248
2006	275	44.125	0.42467
2007	275	43.756	0.46331
2008	275	44.278	0.42489
2010	275	44.669	0.34838
2011	275	44.58	0.3705
2012	275	44.45	0.39777
2013	275	44.825	0.41039
2014	264	44.717	0.41627
2015	264	44.301	0.4492

Appendix 2

Distance-based test for homogeneity of multivariate dispersions (PERMDISP) by Reef Type.

Resemblance worksheet
Name: Resem1
Data type: Similarity
Selection: 1-253,1310-1584,2410-2684,3774-4037
Transform: Fourth root
Resemblance: S17 Bray-Curtis similarity (+d)
Group factor: Y/R
Number of permutations: 9999
Number of groups: 20
Number of samples: 1067
DEVIATIONS FROM CENTROID
F: 14.572 df1: 19 df2: 1047
P(perm): 0.0001
PAIRWISE COMPARISONS

Year/Reef	T	p(Perm)
(2000LMR,2000RC)	6.0859	0.0001
(2000LMR,2000LOR)	2.0724	0.0563
(2000LMR,2000CPS)	0.59814	0.5586
(2000LMR,2000LIR)	2.4041	0.0587
(2000LMR,2005LMR)	3.8694	0.0006
(2000LMR,2005RC)	3.2637	0.0024
(2000LMR,2005LOR)	2.9664	0.0061
(2000LMR,2005CPS)	1.8464	0.0822
(2000LMR,2005LIR)	1.9911	0.1166
(2000LMR,2010LMR)	4.3891	0.0001
(2000LMR,2010RC)	7.9202	0.0001
(2000LMR,2010LOR)	3.5904	0.0009
(2000LMR,2010CPS)	0.95489	0.3652
(2000LMR,2010LIR)	1.4917	0.2325
(2000LMR,2015RC)	6.0818	0.0001
(2000LMR,2015LMR)	6.3328	0.0001
(2000LMR,2015LOR)	4.2253	0.0002
(2000LMR,2015CPS)	1.9493	0.0561
(2000LMR,2015LIR)	2.8792	0.0261
(2000RC,2000LOR)	7.9158	0.0001
(2000RC,2000CPS)	5.1753	0.0001
(2000RC,2000LIR)	1.1585	0.3236
(2000RC,2005LMR)	3.0895	0.002
(2000RC,2005RC)	2.7751	0.0184
(2000RC,2005LOR)	3.9344	0.0004
(2000RC,2005CPS)	8.1102	0.0001
(2000RC,2005LIR)	1.4611	0.1981
(2000RC,2010LMR)	2.9074	0.005
(2000RC,2010RC)	0.35672	0.7768
(2000RC,2010LOR)	3.4143	0.0011
(2000RC,2010CPS)	5.4114	0.0001
(2000RC,2010LIR)	1.8704	0.1043
(2000RC,2015RC)	0.35665	0.7779
(2000RC,2015LMR)	1.1933	0.2606
(2000RC,2015LOR)	2.8814	0.0088
(2000RC,2015CPS)	8.424	0.0001
(2000RC,2015LIR)	0.93336	0.4179
(2000LOR,2000CPS)	2.7613	0.008
(2000LOR,2000LIR)	4.286	0.0032

(2000LOR,2005LMR)	6.1092	0.0001
(2000LOR,2005RC)	5.6803	0.0001
(2000LOR,2005LOR)	5.5616	0.0001
(2000LOR,2005CPS)	0.3832	0.71
(2000LOR,2005LIR)	3.8205	0.0097
(2000LOR,2010LMR)	6.8307	0.0001
(2000LOR,2010RC)	11.168	0.0001
(2000LOR,2010LOR)	6.1804	0.0001
(2000LOR,2010CPS)	3.1288	0.0038
(2000LOR,2010LIR)	3.3461	0.0257
(2000LOR,2015RC)	8.2924	0.0001
(2000LOR,2015LMR)	8.9014	0.0001
(2000LOR,2015LOR)	6.7994	0.0001
(2000LOR,2015CPS)	0.40574	0.6855
(2000LOR,2015LIR)	5.124	0.0007
(2000CPS,2000LIR)	2.1023	0.1188
(2000CPS,2005LMR)	3.0175	0.0028
(2000CPS,2005RC)	2.6184	0.0234
(2000CPS,2005LOR)	2.2191	0.0357
(2000CPS,2005CPS)	2.5332	0.0162
(2000CPS,2005LIR)	1.6954	0.1732
(2000CPS,2010LMR)	3.5016	0.0016
(2000CPS,2010RC)	7.0779	0.0001
(2000CPS,2010LOR)	2.8095	0.0072
(2000CPS,2010CPS)	0.29734	0.8206
(2000CPS,2010LIR)	1.2017	0.3164
(2000CPS,2015RC)	5.2212	0.0001
(2000CPS,2015LMR)	5.3562	0.0001
(2000CPS,2015LOR)	3.4047	0.0009
(2000CPS,2015CPS)	2.7178	0.0158
(2000CPS,2015LIR)	2.6036	0.0598
(2000LIR,2005LMR)	0.41554	0.7307
(2000LIR,2005RC)	0.49191	0.6807
(2000LIR,2005LOR)	1.0185	0.4084
(2000LIR,2005CPS)	4.1295	0.0045
(2000LIR,2005LIR)	0.25399	0.8402
(2000LIR,2010LMR)	0.25594	0.8258
(2000LIR,2010RC)	1.8382	0.1346
(2000LIR,2010LOR)	0.65749	0.5798
(2000LIR,2010CPS)	1.9396	0.1444

(2000LIR,2010LIR)	0.62558	0.6041
(2000LIR,2015RC)	1.065	0.3657
(2000LIR,2015LMR)	0.79226	0.4971
(2000LIR,2015LOR)	0.30001	0.7987
(2000LIR,2015CPS)	4.5764	0.0039
(2000LIR,2015LIR)	0.22931	0.855
(2005LMR,2005RC)	0.16006	0.8865
(2005LMR,2005LOR)	1.0355	0.3247
(2005LMR,2005CPS)	6.1141	0.0001
(2005LMR,2005LIR)	0.01508	0.9895
(2005LMR,2010LMR)	0.3668	0.7345
(2005LMR,2010RC)	4.1545	0.0001
(2005LMR,2010LOR)	0.38562	0.7184
(2005LMR,2010CPS)	2.9601	0.0048
(2005LMR,2010LIR)	0.50125	0.6819
(2005LMR,2015RC)	2.8328	0.0065
(2005LMR,2015LMR)	2.4289	0.0268
(2005LMR,2015LOR)	0.27859	0.797
(2005LMR,2015CPS)	6.3772	0.0001
(2005LMR,2015LIR)	0.78217	0.5167
(2005RC,2005LOR)	0.76794	0.4595
(2005RC,2005CPS)	5.5717	0.0001
(2005RC,2005LIR)	0.10321	0.9308
(2005RC,2010LMR)	0.48882	0.6452
(2005RC,2010RC)	3.9661	0.0007
(2005RC,2010LOR)	0.17854	0.8652
(2005RC,2010CPS)	2.4532	0.0425
(2005RC,2010LIR)	0.41146	0.7202
(2005RC,2015RC)	2.626	0.0241
(2005RC,2015LMR)	2.2985	0.0261
(2005RC,2015LOR)	0.41519	0.6786
(2005RC,2015CPS)	5.9575	0.0001
(2005RC,2015LIR)	0.8685	0.454
(2005LOR,2005CPS)	5.4293	0.0001
(2005LOR,2005LIR)	0.57396	0.6536
(2005LOR,2010LMR)	1.4583	0.1804
(2005LOR,2010RC)	5.4416	0.0001
(2005LOR,2010LOR)	0.6762	0.5205
(2005LOR,2010CPS)	2.0092	0.0649
(2005LOR,2010LIR)	0.0012951	0.9992
(2005LOR,2015RC)	3.7982	0.0005
(2005LOR,2015LMR)	3.5565	0.0009
(2005LOR,2015LOR)	1.3598	0.1962
(2005LOR,2015CPS)	5.7711	0.0001
(2005LOR,2015LIR)	1.4704	0.239
(2005CPS,2005LIR)	3.642	0.0128
(2005CPS,2010LMR)	6.8362	0.0001
(2005CPS,2010RC)	11.22	0.0001
(2005CPS,2010LOR)	6.0928	0.0001
(2005CPS,2010CPS)	2.9494	0.0076
(2005CPS,2010LIR)	3.1131	0.0349
(2005CPS,2015RC)	8.4213	0.0001
(2005CPS,2015LMR)	9.0063	0.0001
(2005CPS,2015LOR)	6.7589	0.0001
(2005CPS,2015CPS)	0.013685	0.9904
(2005CPS,2015LIR)	4.9066	0.0014

(2005LIR,2010LMR)	0.16707	0.8869
(2005LIR,2010RC)	2.2733	0.0637
(2005LIR,2010LOR)	0.22057	0.8612
(2005LIR,2010CPS)	1.5223	0.2288
(2005LIR,2010LIR)	0.36207	0.7619
(2005LIR,2015RC)	1.4079	0.2277
(2005LIR,2015LMR)	1.2051	0.3003
(2005LIR,2015LOR)	0.12882	0.916
(2005LIR,2015CPS)	4.0613	0.0075
(2005LIR,2015LIR)	0.51573	0.6672
(2010LMR,2010RC)	3.9984	0.0003
(2010LMR,2010LOR)	0.77666	0.4705
(2010LMR,2010CPS)	3.447	0.0015
(2010LMR,2010LIR)	0.71816	0.5402
(2010LMR,2015RC)	2.635	0.0116
(2010LMR,2015LMR)	2.1531	0.0522
(2010LMR,2015LOR)	0.081768	0.9396
(2010LMR,2015CPS)	7.1573	0.0001
(2010LMR,2015LIR)	0.63791	0.5993
(2010RC,2010LOR)	4.7452	0.0001
(2010RC,2010CPS)	7.0878	0.0001
(2010RC,2010LIR)	2.9159	0.0219
(2010RC,2015RC)	0.8229	0.4977
(2010RC,2015LMR)	1.9179	0.0656
(2010RC,2015LOR)	4.0444	0.0003
(2010RC,2015CPS)	11.981	0.0001
(2010RC,2015LIR)	1.5724	0.1943
(2010LOR,2010CPS)	2.6484	0.0136
(2010LOR,2010LIR)	0.34872	0.7831
(2010LOR,2015RC)	3.2263	0.0019
(2010LOR,2015LMR)	2.8773	0.0087
(2010LOR,2015LOR)	0.68474	0.5166
(2010LOR,2015CPS)	6.4535	0.0001
(2010LOR,2015LIR)	1.0786	0.374
(2010CPS,2010LIR)	1.0082	0.4011
(2010CPS,2015RC)	5.3485	0.0001
(2010CPS,2015LMR)	5.4409	0.0001
(2010CPS,2015LOR)	3.2989	0.0016
(2010CPS,2015CPS)	3.1055	0.0052
(2010CPS,2015LIR)	2.3954	0.0838
(2010LIR,2015RC)	1.8792	0.1097
(2010LIR,2015LMR)	1.7631	0.1255
(2010LIR,2015LOR)	0.69304	0.5635
(2010LIR,2015CPS)	3.5359	0.0236
(2010LIR,2015LIR)	0.96437	0.3832
(2015RC,2015LMR)	0.81841	0.4337
(2015RC,2015LOR)	2.6441	0.0105
(2015RC,2015CPS)	8.8292	0.0001
(2015RC,2015LIR)	0.81068	0.4865
(2015LMR,2015LOR)	2.1858	0.0383
(2015LMR,2015CPS)	9.4401	0.0001
(2015LMR,2015LIR)	0.46419	0.6977
(2015LOR,2015CPS)	7.135	0.0001
(2015LOR,2015LIR)	0.69295	0.5582
(2015CPS,2015LIR)	5.5136	0.0005

Appendix 3

Distance-based test for homogeneity of multivariate dispersions (PERMDISP) for Reef Type RC

Group factor: Y/R
Number of permutations: 9999
Number of groups: 15
Number of samples: 660
DEVIATIONS FROM CENTROID
F: 2.9428 df1: 14 df2: 645
P(perm): 0.0173

(2000RC,2001RC)	0.24052	0.8468
(2000RC,2002RC)	2.3306	0.0494
(2000RC,2003RC)	3.3186	0.0062
(2000RC,2004RC)	1.7613	0.1515
(2000RC,2005RC)	2.7751	0.0208
(2000RC,2006RC)	0.088482	0.9426
(2000RC,2007RC)	1.1739	0.3461
(2000RC,2008RC)	1.1553	0.3622
(2000RC,2010RC)	0.35672	0.7772
(2000RC,2011RC)	1.3711	0.2636
(2000RC,2012RC)	1.3684	0.2679
(2000RC,2013RC)	0.24195	0.849
(2000RC,2014RC)	0.14853	0.9055
(2000RC,2015RC)	0.35665	0.7771
(2001RC,2002RC)	2.4821	0.0424
(2001RC,2003RC)	3.4153	0.0042
(2001RC,2004RC)	1.9399	0.1195
(2001RC,2005RC)	2.9037	0.0151
(2001RC,2006RC)	0.34006	0.7943
(2001RC,2007RC)	1.3836	0.2975
(2001RC,2008RC)	1.3637	0.3013
(2001RC,2010RC)	0.059578	0.9619
(2001RC,2011RC)	1.569	0.209
(2001RC,2012RC)	1.5657	0.2185
(2001RC,2013RC)	0.017432	0.9896
(2001RC,2014RC)	0.39563	0.7558
(2001RC,2015RC)	0.59648	0.6347
(2002RC,2003RC)	0.94756	0.3854
(2002RC,2004RC)	0.62251	0.5794
(2002RC,2005RC)	0.38372	0.7288
(2002RC,2006RC)	2.435	0.0371
(2002RC,2007RC)	1.3632	0.2529
(2002RC,2008RC)	1.335	0.2616
(2002RC,2010RC)	3.2895	0.005
(2002RC,2011RC)	1.0834	0.3534
(2002RC,2012RC)	1.0695	0.3558
(2002RC,2013RC)	2.7173	0.025
(2002RC,2014RC)	2.3409	0.0463
(2002RC,2015RC)	2.1358	0.0687
(2003RC,2004RC)	1.6199	0.146
(2003RC,2005RC)	0.59613	0.586
(2003RC,2006RC)	3.5579	0.0026
(2003RC,2007RC)	2.4846	0.034
(2003RC,2008RC)	2.4206	0.0379
(2003RC,2010RC)	4.7555	0.0002
(2003RC,2011RC)	2.1391	0.0614
(2003RC,2012RC)	2.113	0.0703
(2003RC,2013RC)	3.8084	0.0016
(2003RC,2014RC)	3.438	0.0032

(2003RC,2015RC)	3.2329	0.0033
(2004RC,2005RC)	1.0409	0.3663
(2004RC,2006RC)	1.8128	0.137
(2004RC,2007RC)	0.71137	0.5615
(2004RC,2008RC)	0.69724	0.5744
(2004RC,2010RC)	2.5674	0.0328
(2004RC,2011RC)	0.4504	0.7002
(2004RC,2012RC)	0.44146	0.7184
(2004RC,2013RC)	2.1145	0.0843
(2004RC,2014RC)	1.7266	0.1545
(2004RC,2015RC)	1.5163	0.206
(2005RC,2006RC)	2.9416	0.0109
(2005RC,2007RC)	1.849	0.1102
(2005RC,2008RC)	1.8052	0.1307
(2005RC,2010RC)	3.9661	0.0008
(2005RC,2011RC)	1.5358	0.1807
(2005RC,2012RC)	1.5166	0.1898
(2005RC,2013RC)	3.214	0.0072
(2005RC,2014RC)	2.8345	0.0146
(2005RC,2015RC)	2.626	0.0246
(2006RC,2007RC)	1.1775	0.3606
(2006RC,2008RC)	1.1554	0.3708
(2006RC,2010RC)	0.49832	0.6896
(2006RC,2011RC)	1.3898	0.2576
(2006RC,2012RC)	1.386	0.2642
(2006RC,2013RC)	0.35236	0.7787
(2006RC,2014RC)	0.065492	0.9588
(2006RC,2015RC)	0.28937	0.8189
(2007RC,2008RC)	0.00025709	0.9998
(2007RC,2010RC)	1.8769	0.1363
(2007RC,2011RC)	0.25249	0.8409
(2007RC,2012RC)	0.25639	0.8375
(2007RC,2013RC)	1.508	0.2475
(2007RC,2014RC)	1.0954	0.3792
(2007RC,2015RC)	0.87205	0.4936
(2008RC,2010RC)	1.8321	0.15
(2008RC,2011RC)	0.24758	0.8455
(2008RC,2012RC)	0.25148	0.843
(2008RC,2013RC)	1.4817	0.2537
(2008RC,2014RC)	1.0753	0.4083
(2008RC,2015RC)	0.85556	0.5062
(2010RC,2011RC)	2.0956	0.0821
(2010RC,2012RC)	2.0841	0.0835
(2010RC,2013RC)	0.088037	0.9429
(2010RC,2014RC)	0.56551	0.6442
(2010RC,2015RC)	0.8229	0.5081
(2011RC,2012RC)	0.0057049	0.9962
(2011RC,2013RC)	1.7075	0.171
(2011RC,2014RC)	1.3074	0.2768

(2011RC,2015RC)	1.0909	0.3625
(2012RC,2013RC)	1.7022	0.1768
(2012RC,2014RC)	1.3043	0.2998
(2012RC,2015RC)	1.0891	0.3757
(2013RC,2014RC)	0.41269	0.7434
(2013RC,2015RC)	0.63298	0.6173
(2014RC,2015RC)	0.22103	0.8616

Appendix 3a

RC site DB1 Distance-based test for homogeneity of multivariate dispersions (PERMDISP)

Group factor: Y/S
Number of permutations: 9999
Number of groups: 15
Number of samples: 165
DEVIATIONS FROM CENTROID
F: 52.537 df1: 14 df2: 150
P(perm): 0.0001

(2000DB1,2001DB1)	0.3737	0.7825
(2000DB1,2002DB1)	2.4053	0.0638
(2000DB1,2003DB1)	0.81085	0.5195
(2000DB1,2004DB1)	0.31137	0.8333
(2000DB1,2005DB1)	0.84796	0.5106
(2000DB1,2006DB1)	6.91	0.0001
(2000DB1,2007DB1)	6.91	0.0001
(2000DB1,2008DB1)	6.91	0.0002
(2000DB1,2010DB1)	6.91	0.0001
(2000DB1,2011DB1)	1.9564	0.1714
(2000DB1,2012DB1)	6.91	0.0001
(2000DB1,2013DB1)	6.91	0.0001
(2000DB1,2014DB1)	6.91	0.0001
(2000DB1,2015DB1)	6.91	0.0001
(2001DB1,2002DB1)	2.1964	0.0738
(2001DB1,2003DB1)	0.49633	0.6735
(2001DB1,2004DB1)	0.69299	0.6096
(2001DB1,2005DB1)	0.49393	0.6846
(2001DB1,2006DB1)	8.5646	0.0001
(2001DB1,2007DB1)	8.5646	0.0001
(2001DB1,2008DB1)	8.5646	0.0001
(2001DB1,2010DB1)	8.5646	0.0001
(2001DB1,2011DB1)	2.4048	0.081
(2001DB1,2012DB1)	8.5646	0.0001
(2001DB1,2013DB1)	8.5646	0.0001
(2001DB1,2014DB1)	8.5646	0.0001
(2001DB1,2015DB1)	8.5646	0.0001
(2002DB1,2003DB1)	1.5086	0.2066
(2002DB1,2004DB1)	2.6581	0.0454
(2002DB1,2005DB1)	1.8551	0.116
(2002DB1,2006DB1)	11.865	0.0001
(2002DB1,2007DB1)	11.865	0.0001
(2002DB1,2008DB1)	11.865	0.0001
(2002DB1,2010DB1)	11.865	0.0001
(2002DB1,2011DB1)	4.2458	0.0033
(2002DB1,2012DB1)	11.865	0.0001
(2002DB1,2013DB1)	11.865	0.0001
(2002DB1,2014DB1)	11.865	0.0001
(2002DB1,2015DB1)	11.865	0.0001
(2003DB1,2004DB1)	1.0964	0.3615
(2003DB1,2005DB1)	0.077942	0.949
(2003DB1,2006DB1)	7.9328	0.0001
(2003DB1,2007DB1)	7.9328	0.0001
(2003DB1,2008DB1)	7.9328	0.0001
(2003DB1,2010DB1)	7.9328	0.0001
(2003DB1,2011DB1)	2.6833	0.0453
(2003DB1,2012DB1)	7.9328	0.0001
(2003DB1,2013DB1)	7.9328	0.0001
(2003DB1,2014DB1)	7.9328	0.0001
(2003DB1,2015DB1)	7.9328	0.0001
(2004DB1,2005DB1)	1.1665	0.4057
(2004DB1,2006DB1)	6.0937	0.0001

(2004DB1,2007DB1)	6.0937	0.0001
(2004DB1,2008DB1)	6.0937	0.0001
(2004DB1,2010DB1)	6.0937	0.0001
(2004DB1,2011DB1)	1.623	0.287
(2004DB1,2012DB1)	6.0937	0.0001
(2004DB1,2013DB1)	6.0937	0.0001
(2004DB1,2014DB1)	6.0937	0.0001
(2004DB1,2015DB1)	6.0937	0.0001
(2005DB1,2006DB1)	10.676	0.0001
(2005DB1,2007DB1)	10.676	0.0001
(2005DB1,2008DB1)	10.676	0.0001
(2005DB1,2010DB1)	10.676	0.0001
(2005DB1,2011DB1)	2.9215	0.0361
(2005DB1,2012DB1)	10.676	0.0001
(2005DB1,2013DB1)	10.676	0.0001
(2005DB1,2014DB1)	10.676	0.0001
(2005DB1,2015DB1)	10.676	0.0001
(2006DB1,2007DB1)	0	0.0001
(2006DB1,2008DB1)	0	0.0001
(2006DB1,2010DB1)	0	0.0001
(2006DB1,2011DB1)	3.2708	0.0001
(2006DB1,2012DB1)	2.394	0.1261
(2006DB1,2013DB1)	2.9635	0.0001
(2006DB1,2014DB1)	3.0685	0.0001
(2006DB1,2015DB1)	5.9235	0.0001
(2007DB1,2008DB1)	0	0.0001
(2007DB1,2010DB1)	0	0.0001

(2007DB1,2011DB1)	3.2708	0.0001
(2007DB1,2012DB1)	2.394	0.1283
(2007DB1,2013DB1)	2.9635	0.0001
(2007DB1,2014DB1)	3.0685	0.0001
(2007DB1,2015DB1)	5.9235	0.0002
(2008DB1,2010DB1)	0	0.0001
(2008DB1,2011DB1)	3.2708	0.0001
(2008DB1,2012DB1)	2.394	0.1279
(2008DB1,2013DB1)	2.9635	0.0001
(2008DB1,2014DB1)	3.0685	0.0001
(2008DB1,2015DB1)	5.9235	0.0001
(2010DB1,2011DB1)	3.2708	0.0001
(2010DB1,2012DB1)	2.394	0.1283
(2010DB1,2013DB1)	2.9635	0.0001
(2010DB1,2014DB1)	3.0685	0.0001
(2010DB1,2015DB1)	5.9235	0.0001
(2011DB1,2012DB1)	3.2708	0.0001
(2011DB1,2013DB1)	3.2708	0.0001
(2011DB1,2014DB1)	3.2708	0.0001
(2011DB1,2015DB1)	3.2708	0.0001
(2012DB1,2013DB1)	2.8573	0.0002
(2012DB1,2014DB1)	3.0428	0.0001
(2012DB1,2015DB1)	5.9182	0.0001
(2013DB1,2014DB1)	2.2716	0.0327
(2013DB1,2015DB1)	5.7651	0.0001
(2014DB1,2015DB1)	5.1788	0.0002

Appendix 4

Reef CPS Distance-based test for homogeneity of multivariate dispersions (PERMDISP)

Transform: Fourth root
Resemblance: S17 Bray-Curtis similarity (+d)
Group factor: Y/R
Number of permutations: 9999
Number of groups: 15
Number of samples: 1089
DEVIATIONS FROM CENTROID
F: 3.2375 df1: 14 df2: 1074
P(perm): 0.0019

Reef type	t	p(perm)
(2000CPS,2001CPS)	0.067489	0.9589
(2000CPS,2002CPS)	3.38	0.0011
(2000CPS,2003CPS)	2.5873	0.0169
(2000CPS,2004CPS)	2.1037	0.056
(2000CPS,2005CPS)	2.5332	0.019
(2000CPS,2006CPS)	0.81636	0.484
(2000CPS,2007CPS)	1.774	0.1195
(2000CPS,2008CPS)	1.9108	0.0993
(2000CPS,2010CPS)	0.29734	0.8146
(2000CPS,2011CPS)	0.57758	0.6533
(2000CPS,2012CPS)	1.1438	0.351
(2000CPS,2013CPS)	3.0633	0.0038
(2000CPS,2014CPS)	2.6613	0.0162
(2000CPS,2015CPS)	2.7178	0.0151
(2001CPS,2002CPS)	3.1769	0.0037
(2001CPS,2003CPS)	2.4859	0.0254
(2001CPS,2004CPS)	2.0468	0.0626
(2001CPS,2005CPS)	2.4404	0.0262
(2001CPS,2006CPS)	0.84603	0.4707
(2001CPS,2007CPS)	1.7405	0.1312
(2001CPS,2008CPS)	1.8711	0.1104
(2001CPS,2010CPS)	0.21204	0.8701
(2001CPS,2011CPS)	0.62108	0.6341
(2001CPS,2012CPS)	1.1538	0.3467
(2001CPS,2013CPS)	2.9215	0.0096
(2001CPS,2014CPS)	2.5465	0.025
(2001CPS,2015CPS)	2.593	0.0192
(2002CPS,2003CPS)	1.3769	0.1819
(2002CPS,2004CPS)	1.7105	0.1049
(2002CPS,2005CPS)	1.3468	0.1987
(2002CPS,2006CPS)	2.9881	0.0062
(2002CPS,2007CPS)	2.0459	0.0518
(2002CPS,2008CPS)	1.7974	0.0972
(2002CPS,2010CPS)	3.6865	0.0009
(2002CPS,2011CPS)	2.8844	0.0109
(2002CPS,2012CPS)	2.5873	0.0194
(2002CPS,2013CPS)	0.88369	0.395
(2002CPS,2014CPS)	1.4417	0.1732
(2002CPS,2015CPS)	1.4773	0.1577
(2003CPS,2004CPS	0.46786	0.6557
(2003CPS,2005CPS)	0.0082229	0.9939
(2003CPS,2006CPS)	1.972	0.0618
(2003CPS,2007CPS)	0.85827	0.4243
(2003CPS,2008CPS)	0.62302	0.5605
(2003CPS,2010CPS)	2.9965	0.0067
(2003CPS,2011CPS)	2.0191	0.0668
(2003CPS,2012CPS)	1.5382	0.1558
(2003CPS,2013CPS)	0.56838	0.5915
(2003CPS,2014CPS)	0.0027303	0.9981
(2003CPS,2015CPS)	0.0051098	0.9949
(2004CPS,2005CPS)	0.45064	0.6723
(2004CPS,2006CPS)	1.459	0.1721
(2004CPS,2007CPS)	0.37668	0.7189
(2004CPS,2008CPS)	0.16294	0.8842
(2004CPS,2010CPS)	2.5207	0.0234
(2004CPS,2011CPS)	1.5538	0.1595
(2004CPS,2012CPS)	1.0477	0.3311
(2004CPS,2013CPS)	1.0108	0.333
(2004CPS,2014CPS)	0.48047	0.6507

(2004CPS,2015CPS)	0.49795	0.6384
(2005CPS,2006CPS)	1.9292	0.0635
(2005CPS,2007CPS)	0.83375	0.4235
(2005CPS,2008CPS)	0.60377	0.5695
(2005CPS,2010CPS)	2.9494	0.0065
(2005CPS,2011CPS)	1.9821	0.0721
(2005CPS,2012CPS)	1.5034	0.1594
(2005CPS,2013CPS)	0.5633	0.5854
(2005CPS,2014CPS)	0.0058478	0.9946
(2005CPS,2015CPS)	0.013685	0.9898
(2006CPS,2007CPS)	1.0849	0.3219
(2006CPS,2008CPS)	1.2629	0.2471
(2006CPS,2010CPS)	1.1968	0.3204
(2006CPS,2011CPS)	0.20643	0.8633
(2006CPS,2012CPS)	0.38705	0.7371
(2006CPS,2013CPS)	2.5085	0.02
(2006CPS,2014CPS)	2.0261	0.0598
(2006CPS,2015CPS)	2.0704	0.0553
(2007CPS,2008CPS)	0.2042	0.8556
(2007CPS,2010CPS)	2.1846	0.0595
(2007CPS,2011CPS)	1.2102	0.2992
(2007CPS,2012CPS)	0.67957	0.5512
(2007CPS,2013CPS)	1.4007	0.1796

(2007CPS,2014CPS)	0.88278	0.4205
(2007CPS,2015CPS)	0.90803	0.3928
(2008CPS,2010CPS)	2.329	0.0474
(2008CPS,2011CPS)	1.3739	0.2515
(2008CPS,2012CPS)	0.86392	0.4569
(2008CPS,2013CPS)	1.149	0.2878
(2008CPS,2014CPS)	0.63933	0.5695
(2008CPS,2015CPS)	0.65887	0.5443
(2010CPS,2011CPS)	0.93827	0.4713
(2010CPS,2012CPS)	1.5368	0.2142
(2010CPS,2013CPS)	3.4684	0.0015
(2010CPS,2014CPS)	3.0581	0.0072
(2010CPS,2015CPS)	3.1055	0.006
(2011CPS,2012CPS)	0.56378	0.6561
(2011CPS,2013CPS)	2.5038	0.0256
(2011CPS,2014CPS)	2.0645	0.071
(2011CPS,2015CPS)	2.1018	0.0631
(2012CPS,2013CPS)	2.0649	0.0584
(2012CPS,2014CPS)	1.5796	0.1623
(2012CPS,2015CPS)	1.6154	0.1453
(2013CPS,2014CPS)	0.59313	0.5811
(2013CPS,2015CPS)	0.59999	0.5712
(2014CPS,2015CPS)	0.0082364	0.9945

Appendix 4a

Reef CPS Site FTL1 Distance-based test for homogeneity of multivariate dispersions (PERMDISP)

Transform: Fourth root
Transform: Fourth root
Resemblance: S17 Bray-Curtis similarity (+d)
Group factor: Y/S
Number of permutations: 9999
Number of groups: 15
Number of samples: 165
DEVIATIONS FROM CENTROID
F: 2.1288 df1: 14 df2: 150
P(perm): 0.0396

Site	t	p(perm)
(2000FTL1,2001FTL1)	1.2852	0.322
(2000FTL1,2002FTL1)	0.60863	0.6132
(2000FTL1,2003FTL1)	0.55206	0.6455
(2000FTL1,2004FTL1)	1.3541	0.2228
(2000FTL1,2005FTL1)	0.010987	0.9922
(2000FTL1,2006FTL1)	0.4686	0.6544
(2000FTL1,2007FTL1)	1.066	0.3278
(2000FTL1,2008FTL1)	0.33616	0.7602
(2000FTL1,2010FTL1)	0.36992	0.7331
(2000FTL1,2011FTL1)	0.44673	0.6848
(2000FTL1,2012FTL1)	1.6352	0.1192
(2000FTL1,2013FTL1)	0.13669	0.9023
(2000FTL1,2014FTL1)	0.70937	0.5187
(2000FTL1,2015FTL1)	2.4403	0.0385
(2001FTL1,2002FTL1)	1.7401	0.1895
(2001FTL1,2003FTL1)	1.7642	0.1703
(2001FTL1,2004FTL1)	2.3841	0.0449
(2001FTL1,2005FTL1)	1.202	0.2632
(2001FTL1,2006FTL1)	1.743	0.1189
(2001FTL1,2007FTL1)	0.46811	0.6854
(2001FTL1,2008FTL1)	0.93812	0.4016
(2001FTL1,2010FTL1)	1.6556	0.1513
(2001FTL1,2011FTL1)	1.5861	0.1755
(2001FTL1,2012FTL1)	0.033686	0.979
(2001FTL1,2013FTL1)	1.394	0.2385
(2001FTL1,2014FTL1	0.60375	0.602
(2001FTL1,2015FTL1)	0.91666	0.4295
(2002FTL1,2003FTL1)	0.12798	0.9165
(2002FTL1,2004FTL1)	0.58492	0.6014
(2002FTL1,2005FTL1)	0.53248	0.6244
(2002FTL1,2006FTL1)	0.25627	0.802
(2002FTL1,2007FTL1)	1.6501	0.1387
(2002FTL1,2008FTL1)	0.88221	0.4286
(2002FTL1,2010FTL1)	0.333	0.7472
(2002FTL1,2011FTL1)	0.1331	0.8994
(2002FTL1,2012FTL1)	2.2061	0.048
(2002FTL1,2013FTL1)	0.47805	0.6833
(2002FTL1,2014FTL1)	1.2298	0.2974
(2002FTL1,2015FTL1)	2.8937	0.0225
(2003FTL1,2004FTL1	0.86022	0.4065
(2003FTL1,2005FTL1	0.46828	0.6571
(2003FTL1,2006FTL1)	0.14112	0.8811
(2003FTL1,2007FTL1)	1.7243	0.1114
(2003FTL1,2008FTL1)	0.8523	0.435
(2003FTL1,2010FTL1)	0.23349	0.8068
(2003FTL1,2011FTL1)	0.02559	0.9841
(2003FTL1,2012FTL1)	2.3518	0.033
(2003FTL1,2013FTL1)	0.40519	0.7093
(2003FTL1,2014FTL1)	1.2299	0.2635
(2003FTL1,2015FTL1)	3.0134	0.0113
(2004FTL1,2005FTL1)	1.1382	0.3336
(2004FTL1,2006FTL1)	1.1276	0.2472
(2004FTL1,2007FTL1)	2.6431	0.0156
(2004FTL1,2008FTL1)	1.5671	0.1548
(2004FTL1,2010FTL1)	1.1875	0.2313
(2004FTL1,2011FTL1)	0.70966	0.5241
(2004FTL1,2012FTL1)	3.335	0.004
(2004FTL1,2013FTL1)	1.199	0.2768
(2004FTL1,2014FTL1)	1.9338	0.0922
(2004FTL1,2015FTL1)	3.7372	0.0037
(2005FTL1,2006FTL1)	0.38773	0.7434
(2005FTL1,2007FTL1)	0.95621	0.4185
(2005FTL1,2008FTL1)	0.31448	0.7864
(2005FTL1,2010FTL1)	0.30602	0.808
(2005FTL1,2011FTL1)	0.39174	0.7534
(2005FTL1,2012FTL1)	1.46	0.2096
(2005FTL1,2013FTL1)	0.1102	0.9284
(2005FTL1,2014FTL1)	0.6561	0.5965
(2005FTL1,2015FTL1)	2.2609	0.0814
(2006FTL1,2007FTL1)	1.7276	0.1038
(2006FTL1,2008FTL1)	0.79206	0.4629
(2006FTL1,2010FTL1)	0.10763	0.9131
(2006FTL1,2011FTL1)	0.085688	0.9346
(2006FTL1,2012FTL1)	2.4027	0.028
(2006FTL1,2013FTL1)	0.31057	0.7729
(2006FTL1,2014FTL1)	1.1899	0.2956
(2006FTL1,2015FTL1)	3.0478	0.0129
(2007FTL1,2008FTL1)	0.62569	0.5835
(2007FTL1,2010FTL1)	1.5937	0.1087
(2007FTL1,2011FTL1)	1.4428	0.187
(2007FTL1,2012FTL1)	0.56896	0.6094
(2007FTL1,2013FTL1	1.2082	0.281
(2007FTL1,2014FTL1)	0.21684	0.845
(2007FTL1,2015FTL1)	1.5921	0.209
(2008FTL1,2010FTL1	0.69981	0.5138
(2008FTL1,2011FTL1)	0.7264	0.5212
(2008FTL1,2012FTL1)	1.1384	0.3254

(2008FTL1,2013FTL1)	0.46094	0.6906
(2008FTL1,2014FTL1)	0.35611	0.7618
(2008FTL1,2015FTL1)	2.0017	0.1224
(2010FTL1,2011FTL1)	0.16249	0.8839
(2010FTL1,2012FTL1)	2.2493	0.0462
(2010FTL1,2013FTL1)	0.21555	0.8427
(2010FTL1,2014FTL1)	1.0947	0.3535
(2010FTL1,2015FTL1)	2.9342	0.0143
(2011FTL1,2012FTL1	1.9742	0.1043
(2011FTL1,2013FTL1)	0.32099	0.7943
(2011FTL1,2014FTL1)	1.0684	0.3966
(2011FTL1,2015FTL1)	2.6988	0.0372
(2012FTL1,2013FTL1)	1.7805	0.1288
(2012FTL1,2014FTL1	0.71017	0.5598
(2012FTL1,2015FTL1)	1.1411	0.3354
(2013FTL1,2014FTL1)	0.83096	0.5112
(2013FTL1,2015FTL1)	2.5572	0.0499
(2014FTL1,2015FTL1)	1.6282	0.2201

Appendix 4b

Reef CPS Site HB1 Distance-based test for homogeneity of multivariate dispersions (PERMDISP)

Resemblance worksheet
Name: Resem14
Data type: Similarity
Selection: 89-99,342-352,595-605,870-880,1145-1155,1420-1430,1695-1705,1970-1980,2245-2255,2520-2530,2795-2805,3070-3080,3345-3355,3609-3619,3873-3883
Transform: Fourth root
Transform: Fourth root
Resemblance: S17 Bray-Curtis similarity (+d)
Group factor: Y/S
Number of permutations: 9999
Number of groups: 15
Number of samples: 165
DEVIATIONS FROM CENTROID
F: 34.261 df1: 14 df2: 150
P(perm): 0.0001

Site/Year	t	p(perm)
(2000HB1,2001HB1)	0.9066	0.3995
(2000HB1,2002HB1)	0.38365	0.7563
(2000HB1,2003HB1)	0.088305	0.9368
(2000HB1,2004HB1)	0.73146	0.5536
(2000HB1,2005HB1)	2.1	0.0641
(2000HB1,2006HB1)	5.6687	0.0001
(2000HB1,2007HB1)	5.6687	0.0001
(2000HB1,2008HB1)	5.6687	0.0001
(2000HB1,2010HB1)	5.6687	0.0001
(2000HB1,2011HB1)	5.6687	0.0001
(2000HB1,2012HB1)	5.6687	0.0001
(2000HB1,2013HB1)	1.7048	0.1026
(2000HB1,2014HB1)	5.6687	0.0001
(2000HB1,2015HB1)	5.6687	0.0001
(2001HB1,2002HB1)	0.65549	0.591
(2001HB1,2003HB1)	0.93303	0.4182
(2001HB1,2004HB1)	0.32096	0.7891
(2001HB1,2005HB1)	1.2026	0.2605
(2001HB1,2006HB1)	7.0073	0.0001
(2001HB1,2007HB1)	7.0073	0.0001
(2001HB1,2008HB1)	7.0073	0.0001
(2001HB1,2010HB1)	7.0073	0.0001
(2001HB1,2011HB1)	7.0073	0.0001
(2001HB1,2012HB1)	7.0073	0.0001
(2001HB1,2013HB1)	2.8202	0.0292
(2001HB1,2014HB1)	7.0073	0.0001
(2001HB1,2015HB1)	7.0073	0.0001
(2002HB1,2003HB1)	0.34552	0.7662
(2002HB1,2004HB1)	0.41651	0.7365
(2002HB1,2005HB1)	2.0252	0.1201
(2002HB1,2006HB1)	8.5166	0.0001

(2002HB1,2007HB1)	8.5166	0.0001
(2002HB1,2008HB1)	8.5166	0.0001
(2002HB1,2010HB1)	8.5166	0.0001
(2002HB1,2011HB1)	8.5166	0.0001
(2002HB1,2012HB1)	8.5166	0.0001
(2002HB1,2013HB1)	2.6278	0.0446
(2002HB1,2014HB1)	8.5166	0.0001
(2002HB1,2015HB1)	8.5166	0.0001
(2003HB1,2004HB1)	0.75747	0.5126
(2003HB1,2005HB1)	2.2758	0.086
(2003HB1,2006HB1)	7.6015	0.0001
(2003HB1,2007HB1)	7.6015	0.0001
(2003HB1,2008HB1)	7.6015	0.0001
(2003HB1,2010HB1)	7.6015	0.0001
(2003HB1,2011HB1)	7.6015	0.0001
(2003HB1,2012HB1)	7.6015	0.0001
(2003HB1,2013HB1)	2.1696	0.0891
(2003HB1,2014HB1)	7.6015	0.0001
(2003HB1,2015HB1)	7.6015	0.0001
(2004HB1,2005HB1)	1.7126	0.1777
(2004HB1,2006HB1)	9.5001	0.0001
(2004HB1,2007HB1)	9.5001	0.0001
(2004HB1,2008HB1)	9.5001	0.0001
(2004HB1,2010HB1)	9.5001	0.0001
(2004HB1,2011HB1)	9.5001	0.0001
(2004HB1,2012HB1)	9.5001	0.0001
(2004HB1,2013HB1)	3.1521	0.0248
(2004HB1,2014HB1)	9.500	0.0001
(2004HB1,2015HB1)	9.5001	0.0001
(2005HB1,2006HB1)	8.6397	0.0001
(2005HB1,2007HB1)	8.6397	0.0001
(2005HB1,2008HB1)	8.6397	0.0001
(2005HB1,2010HB1)	8.6397	0.0001
(2005HB1,2011HB1)	8.6397	0.0001
(2005HB1,2012HB1)	8.6397	0.0001
(2005HB1,2013HB1)	4.2573	0.0004
(2005HB1,2014HB1)	8.6397	0.0001

(2005HB1,2015HB1)	8.6397	0.0001
(2006HB1,2007HB1)	∞	0.0001
(2006HB1,2008HB1)	∞	0.0001
(2006HB1,2010HB1)	∞	0.0001
(2006HB1,2011HB1)	1.3417	1
(2006HB1,2012HB1)	0.35429	0.9955
(2006HB1,2013HB1)	6.192	0.0001
(2006HB1,2014HB1)	1.868	0.143
(2006HB1,2015HB1)	1.737	0.3744
(2007HB1,2008HB1)	∞	0.0001
(2007HB1,2010HB1)	∞	0.0001
(2007HB1,2011HB1)	1.3417	1
(2007HB1,2012HB1)	0.35429	0.9965
(2007HB1,2013HB1)	6.1926	0.0001
(2007HB1,2014HB1)	1.868	0.1407
(2007HB1,2015HB1)	1.737	0.3779
(2008HB1,2010HB1)	∞	0.0001
(2008HB1,2011HB1)	1.3417	1
(2008HB1,2012HB1)	0.35429	0.9959
(2008HB1,2013HB1)	6.1926	0.0001
(2008HB1,2014HB1)	1.868	0.1404
(2008HB1,2015HB1)	1.737	0.3709
(2010HB1,2011HB1)	1.3417	1
(2010HB1,2012HB1)	0.35429	0.996
(2010HB1,2013HB1)	6.1926	0.0001
(2010HB1,2014HB1)	1.868	0.1359
(2010HB1,2015HB1)	1.737	0.3701
(2011HB1,2012HB1)	1.0584	0.4774
(2011HB1,2013HB1)	6.1926	0.0001
(2011HB1,2014HB1)	1.8497	0.1603
(2011HB1,2015HB1)	1.735	0.3669
(2012HB1,2013HB1)	6.1926	0.0001
(2012HB1,2014HB1)	1.8744	0.1453
(2012HB1,2015HB1)	1.7377	0.3726
(2013HB1,2014HB1)	6.1926	0.0001
(2013HB1,2015HB1)	6.1926	0.0001
(2014HB1,2015HB1)	1.5257	0.4762

Appendix 5

Linear Middle Reef Distance-based test for homogeneity of multivariate dispersions (PERMDISP)

Transform: Fourth root
Resemblance: S17 Bray-Curtis similarity (+d)
Group factor: Y/R
Number of permutations: 9999
Number of groups: 15
Number of samples: 1133
DEVIATIONS FROM CENTROID
F: 6.5549 df1: 14 df2: 1118
P(perm): 0.0001

Reef Type/Year	t	p(perm)
(2000LMR,2001LMR)	0.29416	0.
(2000LMR,2002LMR)	1.659	0.141
(2000LMR,2003LMR)	3.4678	0.0014
(2000LMR,2004LMR)	4.7385	0.0001
(2000LMR,2005LMR)	3.8694	0.0006
(2000LMR,2006LMR)	3.7342	0.0008
(2000LMR,2007LMR)	4.7267	0.0001
(2000LMR,2008LMR)	5.2275	0.0001
(2000LMR,2010LMR)	4.3891	0.0003
(2000LMR,2011LMR)	3.8914	0.0008
(2000LMR,2012LMR)	4.0722	0.0005
(2000LMR,2013LMR)	3.9254	0.0006
(2000LMR,2014LMR)	6.4263	0.0001
(2000LMR,2015LMR)	6.3328	0.0001
(2001LMR,2002LMR)	1.8735	0.0961
(2001LMR,2003LMR)	3.6273	0.0019
(2001LMR,2004LMR)	4.852	0.0002
(2001LMR,2005LMR)	4.0168	0.0004
(2001LMR,2006LMR)	3.8857	0.0006
(2001LMR,2007LMR)	4.8456	0.0001
(2001LMR,2008LMR)	5.3272	0.0001
(2001LMR,2010LMR)	4.5182	0.0001
(2001LMR,2011LMR)	4.0378	0.0006
(2001LMR,2012LMR)	4.2124	0.0004
(2001LMR,2013LMR)	4.0706	0.0003
(2001LMR,2014LMR)	6.4499	0.0001
(2001LMR,2015LMR)	6.3691	0.0001
(2002LMR,2003LMR)	1.6308	0.1468
(2002LMR,2004LMR)	2.5497	0.019

(2002LMR,2005LMR)	1.9367	0.0841
(2002LMR,2006LMR)	1.8446	0.0978
(2002LMR,2007LMR)	2.7239	0.0148
(2002LMR,2008LMR)	3.1082	0.0042
(2002LMR,2010LMR)	2.3413	0.0333
(2002LMR,2011LMR)	1.9892	0.0773
(2002LMR,2012LMR)	2.2314	0.0493
(2002LMR,2013LMR)	2.0329	0.0725
(2002LMR,2014LMR)	4.1646	0.0006
(2002LMR,2015LMR)	4.1863	0.0003
(2003LMR,2004LMR)	0.76954	0.4817
(2003LMR,2005LMR)	0.26527	0.8152
(2003LMR,2006LMR)	0.19456	0.8637
(2003LMR,2007LMR)	1.0678	0.3294
(2003LMR,2008LMR)	1.4117	0.1924
(2003LMR,2010LMR)	0.62858	0.5667
(2003LMR,2011LMR)	0.34194	0.7584
(2003LMR,2012LMR)	0.64249	0.5697
(2003LMR,2013LMR)	0.39552	0.7146
(2003LMR,2014LMR)	2.5311	0.0198
(2003LMR,2015LMR)	2.6101	0.0151
(2004LMR,2005LMR)	0.50169	0.6454
(2004LMR,2006LMR)	0.56742	0.5936
(2004LMR,2007LMR)	0.38904	0.7179
(2004LMR,2008LMR)	0.75203	0.4842
(2004LMR,2010LMR)	0.1227	0.908
(2004LMR,2011LMR)	0.4042	0.7047
(2004LMR,2012LMR)	0.045517	0.9648
(2004LMR,2013LMR)	0.3402	0.7488
(2004LMR,2014LMR)	2.0451	0.0532

(2004LMR,2015LMR)	2.1429	0.0444
(2005LMR,2006LMR)	0.068996	0.9512
(2005LMR,2007LMR)	0.82657	0.4488
(2005LMR,2008LMR)	1.1747	0.287
(2005LMR,2010LMR)	0.3668	0.7403
(2005LMR,2011LMR)	0.082721	0.9439
(2005LMR,2012LMR)	0.40017	0.7198
(2005LMR,2013LMR)	0.13929	0.9037
(2005LMR,2014LMR)	2.3433	0.0296
(2005LMR,2015LMR)	2.4289	0.0224
(2006LMR,2007LMR)	0.88352	0.4177
(2006LMR,2008LMR)	1.2277	0.2626
(2006LMR,2010LMR)	0.4322	0.6899
(2006LMR,2011LMR)	0.14955	0.8925
(2006LMR,2012LMR)	0.46057	0.6739
(2006LMR,2013LMR)	0.20496	0.8547
(2006LMR,2014LMR)	2.3729	0.0285
(2006LMR,2015LMR)	2.4576	0.0267
(2007LMR,2008LMR)	0.32248	0.7641
(2007LMR,2010LMR)	0.4857	0.6473
(2007LMR,2011LMR)	0.73178	0.508
(2007LMR,2012LMR)	0.38624	0.731
(2007LMR,2013LMR)	0.67054	0.5541
(2007LMR,2014LMR)	1.5046	0.1652
(2007LMR,2015LMR)	1.6222	0.1365
(2008LMR,2010LMR)	0.83487	0.4404
(2008LMR,2011LMR)	1.0714	0.3288
(2008LMR,2012LMR)	0.7031	0.5323
(2008LMR,2013LMR)	1.0061	0.3566
(2008LMR,2014LMR)	1.2308	0.2554
(2008LMR,2015LMR)	1.3613	0.2084
(2010LMR,2011LMR)	0.27582	0.8042
(2010LMR,2012LMR)	0.063686	0.9555
(2010LMR,2013LMR)	0.21536	0.8501
(2010LMR,2014LMR)	2.056	0.0567
(2010LMR,2015LMR)	2.1531	0.0458
(2011LMR,2012LMR)	0.31607	0.7787
(2011LMR,2013LMR)	0.056246	0.9562
(2011LMR,2014LMR)	2.2193	0.0443
(2011LMR,2015LMR)	2.3096	0.0376
(2012LMR,2013LMR)	0.26005	0.8178
(2012LMR,2014LMR)	1.8082	0.0964
(2012LMR,2015LMR)	1.9123	0.0831
(2013LMR,2014LMR)	2.1466	0.0489
(2013LMR,2015LMR)	2.2396	0.04
(2014LMR,2015LMR)	0.17716	0.8738

Appendix 5a

Distance-based test for homogeneity of multivariate dispersions (PERMDISP) Site FTL2

Resemblance worksheet
Name: Resem1
Data type: Similarity
Selection: 56-66,309-319,562-572,815-825,1090-1100,1365-1375,1640-1650,1915-1925,2190-2200,2465-2475,2740-2750,3015-3025,3290-3300,3554-3564,3818-3828
Transform: Fourth root
Resemblance: S17 Bray-Curtis similarity (+d)
Group factor: Y/S
Number of permutations: 9999
Number of groups: 15
Number of samples: 165
DEVIATIONS FROM CENTROID
F: 3.8278 df1: 14 df2: 150
P(perm): 0.0002

Appendix 5b

Distance-based test for homogeneity of multivariate dispersions (PERMDISP) Site DB2

Resemblance worksheet
Name: Resem1
Data type: Similarity
Selection: 23-33,276-286,529-539,782-792,1057-1067,1332-1342,1607-1617,1882-1892,2157-2167,2432-2442,2707-2717,2982-2992,3257-3267,3521-3531,3785-3795
Transform: Fourth root
Resemblance: S17 Bray-Curtis similarity (+d)
Group factor: Y/S
Number of permutations: 9999
Number of groups: 15
Number of samples: 165
DEVIATIONS FROM CENTROID
F: 2.2335 df1: 14 df2: 150
P(perm): 0.0467

Appendix 6

Linear Outer Reef Distance-based test for homogeneity of multivariate dispersions (PERMDISP)

Group factor: Y/R
Number of permutations: 9999
Number of groups: 15
Number of samples: 990
DEVIATIONS FROM CENTROID
F: 5.474 df1: 14 df2: 975
P(perm): 0.0001

Groups	t	P(perm)
(2000LOR,2001LOR)	1.2297	0.2488
(2000LOR,2002LOR)	5.5576	0.0001
(2000LOR,2003LOR)	6.3205	0.0001
(2000LOR,2004LOR)	6.0494	0.0001
(2000LOR,2005LOR)	4.8513	0.0002
(2000LOR,2006LOR)	4.4005	0.0001
(2000LOR,2007LOR)	4.9697	0.0001
(2000LOR,2008LOR)	4.9366	0.0001
(2000LOR,2010LOR)	5.6294	0.0001
(2000LOR,2011LOR)	5.8871	0.0001
(2000LOR,2012LOR)	5.5444	0.0001
(2000LOR,2013LOR)	5.7065	0.0001
(2000LOR,2014LOR)	5.7638	0.0001
(2000LOR,2015LOR)	6.2669	0.0001

(2001LOR,2002LOR)	4.3451	0.0001
(2001LOR,2003LOR)	5.1852	0.0001
(2001LOR,2004LOR)	4.9278	0.0001
(2001LOR,2005LOR)	3.6876	0.0007
(2001LOR,2006LOR)	3.3307	0.0022
(2001LOR,2007LOR)	3.9131	0.0004
(2001LOR,2008LOR)	3.8587	0.0004
(2001LOR,2010LOR)	4.4828	0.0003
(2001LOR,2011LOR)	4.7375	0.0001
(2001LOR,2012LOR)	4.4356	0.0001
(2001LOR,2013LOR)	4.4794	0.0002
(2001LOR,2014LOR)	4.5834	0.0001
(2001LOR,2015LOR)	5.1284	0.0001
(2002LOR,2003LOR)	1.0609	0.3261
(2002LOR,2004LOR)	0.84646	0.4235

(2002LOR,2005LOR)	0.50967	0.6228
(2002LOR,2006LOR)	0.58367	0.5861
(2002LOR,2007LOR)	0.035963	0.9725
(2002LOR,2008LOR)	0.08318	0.9349
(2002LOR,2010LOR)	0.32964	0.7456
(2002LOR,2011LOR)	0.57345	0.5881
(2002LOR,2012LOR)	0.39614	0.7104
(2002LOR,2013LOR)	0.091121	0.9325
(2002LOR,2014LOR)	0.32991	0.765
(2002LOR,2015LOR)	0.99476	0.3606
(2003LOR,2004LOR)	0.19757	0.8557
(2003LOR,2005LOR)	1.5219	0.1494
(2003LOR,2006LOR)	1.5414	0.1564
(2003LOR,2007LOR)	0.93736	0.3836
(2003LOR,2008LOR)	1.0649	0.3196
(2003LOR,2010LOR)	0.70883	0.5067
(2003LOR,2011LOR)	0.47674	0.6558
(2003LOR,2012LOR)	0.62259	0.5605
(2003LOR,2013LOR)	0.9816	0.3502
(2003LOR,2014LOR)	0.72786	0.4977
(2003LOR,2015LOR)	0.065529	0.9542
(2004LOR,2005LOR)	1.3091	0.2095
(2004LOR,2006LOR)	1.3397	0.2122
(2004LOR,2007LOR)	0.74186	0.4875
(2004LOR,2008LOR)	0.86581	0.4116
(2004LOR,2010LOR)	0.50454	0.6325
(2004LOR,2011LOR)	0.27395	0.798
(2004LOR,2012LOR)	0.42325	0.6962
(2004LOR,2013LOR)	0.76634	0.4628
(2004LOR,2014LOR)	0.51972	0.6239
(2004LOR,2015LOR)	0.13288	0.8992
(2005LOR,2006LOR)	0.10153	0.9242
(2005LOR,2007LOR)	0.49894	0.6487
(2005LOR,2008LOR)	0.38923	0.7154
(2005LOR,2010LOR)	0.81206	0.4465
(2005LOR,2011LOR)	1.0505	0.3306
(2005LOR,2012LOR)	0.86612	0.4169
(2005LOR,2013LOR)	0.60222	0.5677

(2005LOR,2014LOR)	0.82171	0.4337
(2005LOR,2015LOR)	1.4583	0.1698
(2006LOR,2007LOR)	0.56974	0.6004
(2006LOR,2008LOR)	0.46614	0.6627
(2006LOR,2010LOR)	0.86832	0.4157
(2006LOR,2011LOR)	1.0941	0.3101
(2006LOR,2012LOR)	0.91937	0.3965
(2006LOR,2013LOR)	0.67107	0.5285
(2006LOR,2014LOR)	0.8776	0.4071
(2006LOR,2015LOR)	1.4809	0.1637
(2007LOR,2008LOR)	0.11001	0.9183
(2007LOR,2010LOR)	0.26633	0.8129
(2007LOR,2011LOR)	0.48917	0.647
(2007LOR,2012LOR)	0.32923	0.7624
(2007LOR,2013LOR)	0.046318	0.9645
(2007LOR,2014LOR)	0.26496	0.7975
(2007LOR,2015LOR)	0.87631	0.4031
(2008LOR,2010LOR)	0.38573	0.7149
(2008LOR,2011LOR)	0.61179	0.5712
(2008LOR,2012LOR)	0.44694	0.6724
(2008LOR,2013LOR)	0.16751	0.8791
(2008LOR,2014LOR)	0.38651	0.7115
(2008LOR,2015LOR)	1.0032	0.3459
(2010LOR,2011LOR)	0.23477	0.8275
(2010LOR,2012LOR)	0.071771	0.9502
(2010LOR,2013LOR)	0.24452	0.8129
(2010LOR,2014LOR)	0.0062098	0.9953
(2010LOR,2015LOR)	0.64419	0.5303
(2011LOR,2012LOR)	0.1578	0.8816
(2011LOR,2013LOR)	0.49	0.6425
(2011LOR,2014LOR)	0.24538	0.8216
(2011LOR,2015LOR)	0.41156	0.6877
(2012LOR,2013LOR)	0.31348	0.7667
(2012LOR,2014LOR)	0.079125	0.9357
(2012LOR,2015LOR)	0.55911	0.6076
(2013LOR,2014LOR)	0.24308	0.8166
(2013LOR,2015LOR)	0.91489	0.3846
(2014LOR,2015LOR)	0.66212	0.5436

Appendix 6a

Site DB3 Distance-based test for homogeneity of multivariate dispersions (PERMDISP)

Resemblance worksheet
Name: Resem1
Data type: Similarity
Selection: 34-44,287-297,540-550,793-803,1068-1078,1343-1353,1618-1628,1893-1903,2168-2178,2443-2453,2718-2728,2993-3003,3268-3278,3532-3542,3796-3806
Transform: Fourth root
Resemblance: S17 Bray-Curtis similarity (+d)
Group factor: Y/S
Number of permutations: 9999

Number of groups: 15
Number of samples: 165
DEVIATIONS FROM CENTROID
F: 4.3594 df1: 14 df2: 150
P(perm): 0.0001

Year/Site	t	p(Perm)
(2000DB3,2001DB3)	0.86403	0.3961
(2000DB3,2002DB3)	5.1916	0.0001
(2000DB3,2003DB3)	3.883	0.0007
(2000DB3,2004DB3)	3.2971	0.0074
(2000DB3,2005DB3	3.591	0.0021
(2000DB3,2006DB3)	5.1087	0.0001
(2000DB3,2007DB3)	4.8353	0.0001
(2000DB3,2008DB3)	3.8955	0.0003
(2000DB3,2010DB3)	4.4125	0.0003
(2000DB3,2011DB3)	4.7989	0.0001
(2000DB3,2012DB3)	4.8011	0.0001
(2000DB3,2013DB3)	4.063	0.0002
(2000DB3,2014DB3)	4.3544	0.0001
(2000DB3,2015DB3)	3.5979	0.0017
(2001DB3,2002DB3)	3.3719	0.0028
(2001DB3,2003DB3)	2.4515	0.0393
(2001DB3,2004DB3)	2.0695	0.0607
(2001DB3,2005DB3)	2.3294	0.0441
(2001DB3,2006DB3)	3.4129	0.0052
(2001DB3,2007DB3)	3.3391	0.0055
(2001DB3,2008DB3)	2.1675	0.0523
(2001DB3,2010DB3)	2.8024	0.0176
(2001DB3,2011DB3)	2.9594	0.0089
(2001DB3,2012DB3)	2.9614	0.008
(2001DB3,2013DB3)	2.4337	0.0356
(2001DB3,2014DB3)	2.7882	0.023
(2001DB3,2015DB3)	2.1262	0.0592
(2002DB3,2003DB3)	0.9422	0.3769
(2002DB3,2004DB3)	1.1067	0.3334
(2002DB3,2005DB3)	0.75779	0.4805
(2002DB3,2006DB3)	0.26819	0.7884
(2002DB3,2007DB3)	0.44508	0.6701
(2002DB3,2008DB3)	2.3763	0.0155
(2002DB3,2010DB3)	0.69184	0.4929
(2002DB3,2011DB3)	0.86788	0.3612
(2002DB3,2012DB3)	0.86399	0.3814
(2002DB3,2013DB3)	1.4688	0.1389
(2002DB3,2014DB3)	0.62673	0.5205
(2002DB3,2015DB3)	1.661	0.0892
(2003DB3,2004DB3)	0.25728	0.8163
(2003DB3,2005DB3)	0.056594	0.9576
(2003DB3,2006DB3)	1.1067	0.2863
(2003DB3,2007DB3)	1.1807	0.252
(2003DB3,2008DB3)	0.85651	0.3844
(2003DB3,2010DB3)	0.30006	0.7877
(2003DB3,2011DB3)	0.29455	0.7783
(2003DB3,2012DB3)	0.29752	0.764
(2003DB3,2013DB3)	0.28577	0.7892
(2003DB3,2014DB3)	0.32836	0.7657
(2003DB3,2015DB3)	0.54323	0.5985
(2004DB3,2005DB3)	0.28715	0.7973

(2004DB3,2006DB3)	1.2505	0.2492
(2004DB3,2007DB3)	1.3162	0.2389
(2004DB3,2008DB3)	0.42454	0.6821
(2004DB3,2010DB3)	0.53834	0.6213
(2004DB3,2011DB3)	0.55109	0.6143
(2004DB3,2012DB3)	0.55362	0.6221
(2004DB3,2013DB3)	0.035337	0.9728
(2004DB3,2014DB3)	0.55959	0.6052
(2004DB3,2015DB3)	0.21065	0.8429
(2005DB3,2006DB3)	0.92014	0.3682
(2005DB3,2007DB3)	1.0135	0.3391
(2005DB3,2008DB3)	0.79696	0.4388
(2005DB3,2010DB3)	0.20484	0.8442
(2005DB3,2011DB3)	0.18755	0.8589
(2005DB3,2012DB3)	0.19012	0.8615
(2005DB3,2013DB3)	0.31199	0.7691
(2005DB3,2014DB3)	0.23259	0.8199
(2005DB3,2015DB3)	0.54072	0.5945
(2006DB3,2007DB3)	0.19979	0.8434
(2006DB3,2008DB3)	2.3924	0.0198
(2006DB3,2010DB3)	0.88509	0.3759
(2006DB3,2011DB3)	1.0595	0.2694
(2006DB3,2012DB3)	1.056	0.2695
(2006DB3,2013DB3)	1.5976	0.1224
(2006DB3,2014DB3)	0.82117	0.4078
(2006DB3,2015DB3)	1.7752	0.0834
(2007DB3,2008DB3)	2.2432	0.0291

(2007DB3,2010DB3)	0.98093	0.3355
(2007DB3,2011DB3)	1.125	0.2693
(2007DB3,2012DB3)	1.122	0.2824
(2007DB3,2013DB3)	1.5976	0.1226
(2007DB3,2014DB3)	0.92478	0.3486
(2007DB3,2015DB3)	1.7677	0.097
(2008DB3,2010DB3)	1.3645	0.1511
(2008DB3,2011DB3)	1.6312	0.0666
(2008DB3,2012DB3)	1.6351	0.0612
(2008DB3,2013DB3)	0.67561	0.4629
(2008DB3,2014DB3)	1.3539	0.161
(2008DB3,2015DB3)	0.24294	0.7979
(2010DB3,2011DB3)	0.046772	0.9605
(2010DB3,2012DB3)	0.043387	0.9687
(2010DB3,2013DB3)	0.66644	0.5022
(2010DB3,2014DB3)	0.03895	0.9701
(2010DB3,2015DB3)	0.91635	0.3845
(2011DB3,2012DB3)	0.0041031	0.9958
(2011DB3,2013DB3)	0.73262	0.438
(2011DB3,2014DB3)	0.089349	0.9263
(2011DB3,2015DB3)	1.0024	0.3019
(2012DB3,2013DB3)	0.73616	0.4236
(2012DB3,2014DB3)	0.086088	0.9283
(2012DB3,2015DB3)	1.0055	0.3034
(2013DB3,2014DB3)	0.68559	0.4907
(2013DB3,2015DB3)	0.32008	0.7535
(2014DB3,2015DB3)	0.92851	0.3729

Appendix 6b

Site POMP3 Distance-based test for homogeneity of multivariate dispersions (PERMDISP)

Resemblance worksheet
Name: Resem14
Data type: Similarity
Selection: 210-220,463-473,716-726,991-1001,1266-1276,1541-1551,1816-1826,2091-2101,2366-2376,2641-2651,2916-2926,3191-3201,3466-3476,3730-3740,3994-4004
Transform: Fourth root
Transform: Fourth root
Resemblance: S17 Bray-Curtis similarity (+d)
Group factor: Y/S
Number of permutations: 9999
Number of groups: 15
Number of samples: 165
DEVIATIONS FROM CENTROID
F: 2.1592 df1: 14 df2: 150
P(perm): 0.0399

Year/Site	t	p(Perm)
(2000POMP3,2001POMP3)	0.37888	0.7497
(2000POMP3,2002POMP3)	0.96221	0.4398
(2000POMP3,2003POMP3)	2.2545	0.0973
(2000POMP3,2004POMP3)	2.2883	0.0973
(2000POMP3,2005POMP3)	2.2998	0.1048
(2000POMP3,2006POMP3)	1.0233	0.4207
(2000POMP3,2007POMP3)	1.4806	0.2488
(2000POMP3,2008POMP3)	1.4642	0.2693
(2000POMP3,2010POMP3)	2.3263	0.0802
(2000POMP3,2011POMP3)	2.2599	0.0972
(2000POMP3,2012POMP3)	2.613	0.055
(2000POMP3,2013POMP3)	2.4504	0.0747
(2000POMP3,2014POMP3)	2.3698	0.0891
(2000POMP3,2015POMP3)	2.1688	0.116
(2001POMP3,2002POMP3)	0.98385	0.3052
(2001POMP3,2003POMP3)	2.8985	0.0133
(2001POMP3,2004POMP3)	3.1354	0.007
(2001POMP3,2005POMP3)	2.9484	0.0151
(2001POMP3,2006POMP3)	0.96245	0.3626
(2001POMP3,2007POMP3)	1.602	0.1352
(2001POMP3,2008POMP3)	1.5224	0.1785
(2001POMP3,2010POMP3)	2.9604	0.0091
(2001POMP3,2011POMP3)	2.7286	0.0257
(2001POMP3,2012POMP3)	3.1217	0.0125
(2001POMP3,2013POMP3)	3.128	0.0085
(2001POMP3,2014POMP3)	3.3092	0.0057
(2001POMP3,2015POMP3)	2.7343	0.0179
(2002POMP3,2003POMP3)	2.2637	0.0414
(2002POMP3,2004POMP3)	2.4704	0.027
(2002POMP3,2005POMP3)	2.3242	0.0433
(2002POMP3,2006POMP3)	0.2891	0.7749
(2002POMP3,2007POMP3)	0.96994	0.3332
(2002POMP3,2008POMP3)	0.95518	0.3829
(2002POMP3,2010POMP3)	2.3463	0.0305
(2002POMP3,2011POMP3)	2.1478	0.0687
(2002POMP3,2012POMP3)	2.6003	0.0254
(2002POMP3,2013POMP3)	.5327	0.0301
(2002POMP3,2014POMP3)	2.6554	0.0169
(2002POMP3,2015POMP3)	2.098	0.0533
(2003POMP3,2004POMP3)	0.10805	0.9202
(2003POMP3,2005POMP3)	0.082382	0.9418
(2003POMP3,2006POMP3)	1.4143	0.1923
(2003POMP3,2007POMP3)	0.79754	0.4502
(2003POMP3,2008POMP3)	0.61969	0.5776
(2003POMP3,2010POMP3)	0.14556	0.8865

(2003POMP3,2011POMP3)	0.19395	0.8728
(2003POMP3,2012POMP3)	0.76278	0.4872
(2003POMP3,2013POMP3)	0.33532	0.757
(2003POMP3,2014POMP3)	0.013821	0.9906
(2003POMP3,2015POMP3)	0.087122	0.9335
(2004POMP3,2005POMP3)	0.19713	0.8613
(2004POMP3,2006POMP3)	1.4277	0.186
(2004POMP3,2007POMP3)	0.76518	0.4503
(2004POMP3,2008POMP3)	0.57521	0.616
(2004POMP3,2010POMP3)	0.2639	0.7949
(2004POMP3,2011POMP3)	0.30259	0.7911
(2004POMP3,2012POMP3)	0.89873	0.4309
(2004POMP3,2013POMP3)	0.46965	0.6563
(2004POMP3,2014POMP3)	0.10907	0.9089
(2004POMP3,2015POMP3)	0.0097012	0.9909
(2005POMP3,2006POMP3)	1.4736	0.1863
(2005POMP3,2007POMP3)	0.86189	0.4103
(2005POMP3,2008POMP3)	0.6794	0.5575
(2005POMP3,2010POMP3)	0.063864	0.9518
(2005POMP3,2011POMP3)	0.11903	0.9127
(2005POMP3,2012POMP3)	0.68888	0.5444
(2005POMP3,2013POMP3)	0.2525	0.8131
(2005POMP3,2014POMP3)	0.10578	0.9209
(2005POMP3,2015POMP3)	0.16686	0.8766
(2006POMP3,2007POMP3)	0.54589	0.5939
(2006POMP3,2008POMP3)	0.58762	0.5877
(2006POMP3,2010POMP3)	1.5111	0.1727

(2006POMP3,2011POMP3)	1.4607	0.1928
(2006POMP3,2012POMP3)	1.9014	0.0954
(2006POMP3,2013POMP3)	1.6656	0.132
(2006POMP3,2014POMP3)	1.5262	0.1625
(2006POMP3,2015POMP3)	1.3161	0.2282
(2007POMP3,2008POMP3)	0.087574	0.9385
(2007POMP3,2010POMP3)	0.90702	0.3559
(2007POMP3,2011POMP3)	0.8989	0.4038
(2007POMP3,2012POMP3)	1.3711	0.2071
(2007POMP3,2013POMP3)	1.066	0.3256
(2007POMP3,2014POMP3)	0.85487	0.4109
(2007POMP3,2015POMP3)	0.70959	0.4875
(2008POMP3,2010POMP3)	0.72293	0.5171
(2008POMP3,2011POMP3)	0.7313	0.5185
(2008POMP3,2012POMP3)	1.1788	0.3137
(2008POMP3,2013POMP3)	0.86834	0.4457
(2008POMP3,2014POMP3)	0.65154	0.5724
(2008POMP3,2015POMP3)	0.54388	0.6368
(2010POMP3,2011POMP3)	0.059899	0.9601
(2010POMP3,2012POMP3)	0.6274	0.573
(2010POMP3,2013POMP3)	0.18638	0.8671
(2010POMP3,2014POMP3)	0.17549	0.8674
(2010POMP3,2015POMP3)	0.22745	0.8209
(2011POMP3,2012POMP3)	0.53544	0.6357
(2011POMP3,2013POMP3)	0.11157	0.9194
(2011POMP3,2014POMP3)	0.2237	0.8454

Appendix 7

lme and *Tukey-s post-hoc* of *Aiolochroia crassa*

```
Linear mixed-effects model fit by REML
 Data: ac
       AIC      BIC    logLik
  6827.627 6845.281 -3409.813

Random effects:
 Formula: ~1 | LOCATION
        (Intercept) Residual
StdDev:    39.91091  61.8527

Fixed effects: AREA ~ YEAR
                Value Std.Error  DF   t-value   p-value
(Intercept) -5021.949 1175.1708 593 -4.273378         0
YEAR            2.538    0.5857 593  4.333103         0
 Correlation:
     (Intr)
YEAR -1

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.9583692 -0.5009039 -0.1198661  0.3860578  6.3866242

Number of Observations: 612
Number of Groups: 18
Multiple Comparisons of Means: Tukey Contrasts


Fit: lme.formula(fixed = AREA ~ YEAR, data = ac, random = ~1 | LOCATION)

                   Simultaneous Tests for General Linear Hypotheses

Multiple Comparisons of Means: Tukey Contrasts


Fit: lme.formula(fixed = AREA ~ YEAR, data = ac, random = (~1 | LOCATION))

Linear Hypotheses:
                 Estimate Std. Error z value Pr(>|z|)
2001 - 2000 == 0  9.15410   14.23062   0.643   0.5201
2002 - 2000 == 0  7.32008   14.73501   0.497   0.6193
2003 - 2000 == 0 12.56970   14.95164   0.841   0.4005
2004 - 2000 == 0  9.90543   14.88291   0.666   0.5057
2005 - 2000 == 0  9.16464   15.03522   0.610   0.5422
2006 - 2000 == 0 13.82503   15.22841   0.908   0.3640
2007 - 2000 == 0 18.33016   15.10338   1.214   0.2249
2008 - 2000 == 0 21.52300   14.74633   1.460   0.1444
2010 - 2000 == 0 30.25638   15.09203   2.005   0.0450 *
2011 - 2000 == 0 37.09403   15.17433   2.445   0.0145 *
2012 - 2000 == 0 38.21606   15.33436   2.492   0.0127 *
2013 - 2000 == 0 33.32187   15.32069   2.175   0.0296 *
```

2014 - 2000 == 0	37.16829	15.69856	2.368	0.0179	*
2015 - 2000 == 0	32.46157	16.06610	2.021	0.0433	*
2002 - 2001 == 0	-1.83402	14.32982	-0.128	0.8982	
2003 - 2001 == 0	3.41561	14.54154	0.235	0.8143	
2004 - 2001 == 0	0.75133	14.47789	0.052	0.9586	
2005 - 2001 == 0	0.01054	14.63564	0.001	0.9994	
2006 - 2001 == 0	4.67093	14.84327	0.315	0.7530	
2007 - 2001 == 0	9.17606	14.71889	0.623	0.5330	
2008 - 2001 == 0	12.36890	14.35006	0.862	0.3887	
2010 - 2001 == 0	21.10229	14.70860	1.435	0.1514	
2011 - 2001 == 0	27.93993	14.79160	1.889	0.0589	.
2012 - 2001 == 0	29.06197	14.97034	1.941	0.0522	.
2013 - 2001 == 0	24.16778	14.94185	1.617	0.1058	
2014 - 2001 == 0	28.01420	15.32666	1.828	0.0676	.
2015 - 2001 == 0	23.30747	15.69770	1.485	0.1376	
2003 - 2002 == 0	5.24962	13.03187	0.403	0.6871	
2004 - 2002 == 0	2.58535	13.03003	0.198	0.8427	
2005 - 2002 == 0	1.84456	13.27341	0.139	0.8895	
2006 - 2002 == 0	6.50495	13.50563	0.482	0.6301	
2007 - 2002 == 0	11.01008	13.37314	0.823	0.4103	
2008 - 2002 == 0	14.20292	12.98911	1.093	0.2742	
2010 - 2002 == 0	22.93630	13.33882	1.720	0.0855	.
2011 - 2002 == 0	29.77395	13.42074	2.219	0.0265	*
2012 - 2002 == 0	30.89598	13.63539	2.266	0.0235	*
2013 - 2002 == 0	26.00179	13.62421	1.908	0.0563	.
2014 - 2002 == 0	29.84821	14.06405	2.122	0.0338	*
2015 - 2002 == 0	25.14149	14.43727	1.741	0.0816	.
2004 - 2003 == 0	-2.66427	13.18039	-0.202	0.8398	
2005 - 2003 == 0	-3.40506	13.42094	-0.254	0.7997	
2006 - 2003 == 0	1.25533	13.63154	0.092	0.9266	
2007 - 2003 == 0	5.76046	13.52168	0.426	0.6701	
2008 - 2003 == 0	8.95330	13.14472	0.681	0.4958	
2010 - 2003 == 0	17.68668	13.47363	1.313	0.1893	
2011 - 2003 == 0	24.52433	13.55001	1.810	0.0703	.
2012 - 2003 == 0	25.64636	13.77407	1.862	0.0626	.
2013 - 2003 == 0	20.75217	13.75919	1.508	0.1315	
2014 - 2003 == 0	24.59859	14.19957	1.732	0.0832	.
2015 - 2003 == 0	19.89187	14.56177	1.366	0.1719	
2005 - 2004 == 0	-0.74079	13.40642	-0.055	0.9559	
2006 - 2004 == 0	3.91960	13.64374	0.287	0.7739	
2007 - 2004 == 0	8.42473	13.49787	0.624	0.5325	
2008 - 2004 == 0	11.61757	13.12032	0.885	0.3759	
2010 - 2004 == 0	20.35095	13.46656	1.511	0.1307	
2011 - 2004 == 0	27.18860	13.54347	2.008	0.0447	*
2012 - 2004 == 0	28.31063	13.74558	2.060	0.0394	*
2013 - 2004 == 0	23.41644	13.73136	1.705	0.0881	.
2014 - 2004 == 0	27.26286	14.16435	1.925	0.0543	.
2015 - 2004 == 0	22.55614	14.53631	1.552	0.1207	
2006 - 2005 == 0	4.66039	13.82479	0.337	0.7360	
2007 - 2005 == 0	9.16552	13.73850	0.667	0.5047	
2008 - 2005 == 0	12.35836	13.36795	0.924	0.3552	
2010 - 2005 == 0	21.09174	13.70704	1.539	0.1239	
2011 - 2005 == 0	27.92939	13.78192	2.027	0.0427	*
2012 - 2005 == 0	29.05142	13.98631	2.077	0.0378	*

```
2013 - 2005 == 0 24.15723   13.97167   1.729   0.0838 .
2014 - 2005 == 0 28.00365   14.39733   1.945   0.0518 .
2015 - 2005 == 0 23.29693   14.76284   1.578   0.1145
2007 - 2006 == 0  4.50513   13.95603   0.323   0.7468
2008 - 2006 == 0  7.69797   13.59271   0.566   0.5712
2010 - 2006 == 0 16.43135   13.91853   1.181   0.2378
2011 - 2006 == 0 23.26900   13.98563   1.664   0.0962 .
2012 - 2006 == 0 24.39103   14.19698   1.718   0.0858 .
2013 - 2006 == 0 19.49684   14.18578   1.374   0.1693
2014 - 2006 == 0 23.34326   14.62620   1.596   0.1105
2015 - 2006 == 0 18.63654   14.98480   1.244   0.2136
2008 - 2007 == 0  3.19284   13.41635   0.238   0.8119
2010 - 2007 == 0 11.92622   13.74727   0.868   0.3856
2011 - 2007 == 0 18.76387   13.82176   1.358   0.1746
2012 - 2007 == 0 19.88590   14.01131   1.419   0.1558
2013 - 2007 == 0 14.99171   14.00820   1.070   0.2845
2014 - 2007 == 0 18.83813   14.45452   1.303   0.1925
2015 - 2007 == 0 14.13141   14.82382   0.953   0.3404
2010 - 2008 == 0  8.73338   13.34028   0.655   0.5127
2011 - 2008 == 0 15.57103   13.42240   1.160   0.2460
2012 - 2008 == 0 16.69306   13.61221   1.226   0.2201
2013 - 2008 == 0 11.79887   13.60843   0.867   0.3859
2014 - 2008 == 0 15.64529   14.05879   1.113   0.2658
2015 - 2008 == 0 10.93857   14.43325   0.758   0.4485
2011 - 2010 == 0  6.83765   13.70575   0.499   0.6179
2012 - 2010 == 0  7.95968   13.88922   0.573   0.5666
2013 - 2010 == 0  3.06549   13.88982   0.221   0.8253
2014 - 2010 == 0  6.91191   14.32835   0.482   0.6295
2015 - 2010 == 0  2.20519   14.68990   0.150   0.8807
2012 - 2011 == 0  1.12203   13.96968   0.080   0.9360
2013 - 2011 == 0 -3.77216   13.97050  -0.270   0.7872
2014 - 2011 == 0  0.07426   14.41050   0.005   0.9959
2015 - 2011 == 0 -4.63246   14.76930  -0.314   0.7538
2013 - 2012 == 0 -4.89419   14.13979  -0.346   0.7292
2014 - 2012 == 0 -1.04777   14.56991  -0.072   0.9427
2015 - 2012 == 0 -5.75449   14.93033  -0.385   0.6999
2014 - 2013 == 0  3.84642   14.56047   0.264   0.7916
2015 - 2013 == 0 -0.86030   14.92111  -0.058   0.9540
2015 - 2014 == 0 -4.70672   15.27209  -0.308   0.7579
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Adjusted p values reported -- none method)
```

Appendix 8

lme Amphimedon compressa

```
Linear mixed-effects model fit by REML
 Data: amp
       AIC      BIC    logLik
  14429.62 14450.63 -7210.812

Random effects:
 Formula: ~1 | LOCATION
        (Intercept) Residual
StdDev:    74.91044 37.81315

Fixed effects: AREA ~ YEAR
               Value Std.Error   DF    t-value p-value
(Intercept) 437.5668  490.6675 1377  0.8917786  0.3727
YEAR         -0.1913    0.2446 1377 -0.7822349  0.4342
 Correlation:
     (Intr)
YEAR -1

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-3.1085364 -0.5805756 -0.2407819  0.2372128  6.8977253

Number of Observations: 1413
Number of Groups: 35
```

Appendix 9

lme and *Tukey-s post-hoc* of *Desmapsamma anchorata*

```
Linear mixed-effects model fit by REML
 Data: des22
      AIC      BIC    logLik
  2244.444 2257.657 -1118.222

Random effects:
 Formula: ~1 | LOCATION
        (Intercept) Residual
StdDev:    13.75556 60.20113

Fixed effects: AREA ~ YEAR
              Value     Std.Error   DF   t-value    p-value
(Intercept) 5808.355    2461.1582   190  2.360009   0.0193
YEAR          -2.870       1.2272   190 -2.338703   0.0204
 Correlation:
     (Intr)
YEAR -1

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.1483146 -0.6386590 -0.3258341  0.2293132  3.8618227

Number of Observations: 203
Number of Groups: 12


Multiple Comparisons of Means: Tukey Contrasts


Fit: lme.formula(fixed = AREA ~ YEAR, data = des, random = (~1 | LOCATION))

Linear Hypotheses:
                 Estimate Std. Error z value Pr(>|z|)
2001 - 2000 == 0  -0.01275   19.77280  -0.001  0.99949
2002 - 2000 == 0  -4.72138   19.16610  -0.246  0.80542
2003 - 2000 == 0 -16.25408   19.96326  -0.814  0.41553
2004 - 2000 == 0  17.78047   20.38756   0.872  0.38314
2005 - 2000 == 0 -33.08492   19.11291  -1.731  0.08345 .
2006 - 2000 == 0   0.77259   20.10509   0.038  0.96935
2007 - 2000 == 0 -49.48207   21.61266  -2.289  0.02205 *
2008 - 2000 == 0 -16.94517   27.42779  -0.618  0.53670
2010 - 2000 == 0 -36.43021   22.80717  -1.597  0.11020
2011 - 2000 == 0 -18.92329   27.46573  -0.689  0.49084
2013 - 2000 == 0 -41.21111   30.91154  -1.333  0.18247
2014 - 2000 == 0 -48.65956   29.11768  -1.671  0.09470 .
2015 - 2000 == 0  13.60526   37.83875   0.360  0.71918
2002 - 2001 == 0  -4.70862   18.98270  -0.248  0.80410
2003 - 2001 == 0 -16.24133   19.75099  -0.822  0.41090
2004 - 2001 == 0  17.79322   20.27431   0.878  0.38015
2005 - 2001 == 0 -33.07217   19.03456  -1.737  0.08230 .
```

```
2006 - 2001 == 0   0.78535   19.91329   0.039  0.96854
2007 - 2001 == 0 -49.46931   21.41047  -2.311  0.02086 *
2008 - 2001 == 0 -16.93242   27.23465  -0.622  0.53412
2010 - 2001 == 0 -36.41745   22.57079  -1.613  0.10664
2011 - 2001 == 0 -18.91053   27.27577  -0.693  0.48812
2013 - 2001 == 0 -41.19836   30.81447  -1.337  0.18123
2014 - 2001 == 0 -48.64680   29.03414  -1.676  0.09384 .
2015 - 2001 == 0  13.61801   37.73298   0.361  0.71817
2003 - 2002 == 0 -11.53271   18.61043  -0.620  0.53546
2004 - 2002 == 0  22.50184   19.23521   1.170  0.24207
2005 - 2002 == 0 -28.36355   17.96135  -1.579  0.11430
2006 - 2002 == 0   5.49397   18.92046   0.290  0.77153
2007 - 2002 == 0 -44.76069   20.43564  -2.190  0.02850 *
2008 - 2002 == 0 -12.22380   26.59087  -0.460  0.64573
2010 - 2002 == 0 -31.70883   21.69111  -1.462  0.14379
2011 - 2002 == 0 -14.20191   26.55432  -0.535  0.59277
2013 - 2002 == 0 -36.48974   30.36302  -1.202  0.22945
2014 - 2002 == 0 -43.93818   28.53166  -1.540  0.12357
2015 - 2002 == 0  18.32663   37.31616   0.491  0.62334
2004 - 2003 == 0  34.03455   19.15914   1.776  0.07566 .
2005 - 2003 == 0 -16.83084   17.85017  -0.943  0.34573
2006 - 2003 == 0  17.02667   18.68772   0.911  0.36223
2007 - 2003 == 0 -33.22799   20.43953  -1.626  0.10402
2008 - 2003 == 0  -0.69109   26.70846  -0.026  0.97936
2010 - 2003 == 0 -20.17612   21.78462  -0.926  0.35436
2011 - 2003 == 0  -2.66920   26.57886  -0.100  0.92001
2013 - 2003 == 0 -24.95703   30.49627  -0.818  0.41315
2014 - 2003 == 0 -32.40548   28.59895  -1.133  0.25717
2015 - 2003 == 0  29.85934   37.40947   0.798  0.42477
2005 - 2004 == 0 -50.86539   18.56150  -2.740  0.00614 **
2006 - 2004 == 0 -17.00788   19.44045  -0.875  0.38164
2007 - 2004 == 0 -67.26254   21.07533  -3.192  0.00142 **
2008 - 2004 == 0 -34.72564   27.17569  -1.278  0.20131
2010 - 2004 == 0 -54.21067   22.36086  -2.424  0.01534 *
2011 - 2004 == 0 -36.70375   27.04891  -1.357  0.17480
2013 - 2004 == 0 -58.99158   30.93695  -1.907  0.05654 .
2014 - 2004 == 0 -66.44003   29.07287  -2.285  0.02230 *
2015 - 2004 == 0  -4.17521   37.75915  -0.111  0.91195
2006 - 2005 == 0  33.85751   18.07154   1.874  0.06100 .
2007 - 2005 == 0 -16.39715   19.51776  -0.840  0.40084
2008 - 2005 == 0  16.13975   26.31941   0.613  0.53973
2010 - 2005 == 0  -3.34529   21.31509  -0.157  0.87529
2011 - 2005 == 0  14.16163   26.19729   0.541  0.58880
2013 - 2005 == 0  -8.12619   30.14334  -0.270  0.78748
2014 - 2005 == 0 -15.57464   28.22624  -0.552  0.58110
2015 - 2005 == 0  46.69018   37.12760   1.258  0.20855
2007 - 2006 == 0 -50.25466   20.08174  -2.503  0.01233 *
2008 - 2006 == 0 -17.71776   26.72909  -0.663  0.50742
2010 - 2006 == 0 -37.20280   21.88771  -1.700  0.08919 .
2011 - 2006 == 0 -19.69588   26.61233  -0.740  0.45924
2013 - 2006 == 0 -41.98371   30.43515  -1.379  0.16776
2014 - 2006 == 0 -49.43215   28.50078  -1.734  0.08284 .
2015 - 2006 == 0  12.83267   37.39387   0.343  0.73147
2008 - 2007 == 0  32.53690   27.63485   1.177  0.23904
```

```
2010 - 2007 == 0  13.05186   22.94516   0.569  0.56947
2011 - 2007 == 0  30.55878   27.52802   1.110  0.26696
2013 - 2007 == 0   8.27095   31.24914   0.265  0.79126
2014 - 2007 == 0   0.82251   29.39426   0.028  0.97768
2015 - 2007 == 0  63.08733   38.05059   1.658  0.09732 .
2010 - 2008 == 0 -19.48504   27.98630  -0.696  0.48628
2011 - 2008 == 0  -1.97812   31.82931  -0.062  0.95045
2013 - 2008 == 0 -24.26594   34.98797  -0.694  0.48796
2014 - 2008 == 0 -31.71439   33.79100  -0.939  0.34796
2015 - 2008 == 0  30.55043   41.47436   0.737  0.46136
2011 - 2010 == 0  17.50692   28.01142   0.625  0.53198
2013 - 2010 == 0  -4.78091   31.66680  -0.151  0.88000
2014 - 2010 == 0 -12.22935   30.24111  -0.404  0.68592
2015 - 2010 == 0  50.03547   38.63396   1.295  0.19528
2013 - 2011 == 0 -22.28783   35.12689  -0.634  0.52576
2014 - 2011 == 0 -29.73627   33.77565  -0.880  0.37864
2015 - 2011 == 0  32.52855   41.56338   0.783  0.43385
2014 - 2013 == 0  -7.44844   36.18830  -0.206  0.83693
2015 - 2013 == 0  54.81637   43.50534   1.260  0.20767
2015 - 2014 == 0  62.26482   42.05830   1.480  0.13876
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Adjusted p values reported -- none method)
```

Appendix 10

Ircinia strobilina lme and *Tukey-s post-hoc*

```
Linear mixed-effects model fit by REML
 Data: is
      AIC      BIC    logLik
  4853.811 4869.885 -2422.905

Random effects:
 Formula: ~1 | LOCATION
        (Intercept) Residual
StdDev:    29.01337 83.85871

Fixed effects: AREA ~ YEAR
               Value      Std.Error      DF   t-value p-value
(Intercept) -5913.327 2124.9602     381 -2.782794  0.0057
YEAR            2.988       1.0591      381  2.820950  0.0050
 Correlation:
     (Intr)
YEAR -1

Standardized Within-Group Residuals:
       Min          Q1         Med          Q3         Max
-2.0086213 -0.5356431 -0.1778708  0.3104716  4.7258569
Number of Observations: 413
Number of Groups: 31
Simultaneous Tests for General Linear Hypotheses
Multiple Comparisons of Means: Tukey Contrasts
Fit: lme.formula(fixed = AREA ~ YEAR, data = is, random = list(~1 |
    LOCATION))
Linear Hypotheses:
                Estimate Std. Error z value Pr(>|z|)
2001 - 2000 == 0  -0.3553    25.6135  -0.014   0.9889
2002 - 2000 == 0   1.7130    26.6050   0.064   0.9487
2003 - 2000 == 0 -11.6520    24.8592  -0.469   0.6393
2004 - 2000 == 0  -5.7662    24.6429  -0.234   0.8150
2005 - 2000 == 0  -4.5155    24.4063  -0.185   0.8532
2006 - 2000 == 0  -0.8015    24.5515  -0.033   0.9740
2007 - 2000 == 0   5.6692    25.0497   0.226   0.8210
2008 - 2000 == 0   7.9878    25.0763   0.319   0.7501
2010 - 2000 == 0  14.2268    26.0327   0.546   0.5847
2011 - 2000 == 0  19.1924    26.3887   0.727   0.4670
2012 - 2000 == 0  18.2090    26.2796   0.693   0.4884
2013 - 2000 == 0  24.4735    26.2984   0.931   0.3521
2014 - 2000 == 0  36.7635    30.0296   1.224   0.2209
2015 - 2000 == 0  50.3066    31.3202   1.606   0.1082
2002 - 2001 == 0   2.0684    24.9873   0.083   0.9340
2003 - 2001 == 0 -11.2966    23.0704  -0.490   0.6244
2004 - 2001 == 0  -5.4109    22.8732  -0.237   0.8130
2005 - 2001 == 0  -4.1602    22.6144  -0.184   0.8540
2006 - 2001 == 0  -0.4461    22.7348  -0.020   0.9843
2007 - 2001 == 0   6.0245    23.3118   0.258   0.7961
2008 - 2001 == 0   8.3432    23.3100   0.358   0.7204
```

2010 - 2001 == 0	14.5821	24.2241	0.602	0.5472	
2011 - 2001 == 0	19.5478	24.6405	0.793	0.4276	
2012 - 2001 == 0	18.5643	24.5586	0.756	0.4497	
2013 - 2001 == 0	24.8288	24.5806	1.010	0.3124	
2014 - 2001 == 0	37.1189	28.5202	1.301	0.1931	
2015 - 2001 == 0	50.6620	29.9103	1.694	0.0903	.
2003 - 2002 == 0	-13.3650	23.1323	-0.578	0.5634	
2004 - 2002 == 0	-7.4793	22.9245	-0.326	0.7442	
2005 - 2002 == 0	-6.2286	22.7258	-0.274	0.7840	
2006 - 2002 == 0	-2.5145	22.9297	-0.110	0.9127	
2007 - 2002 == 0	3.9561	23.4829	0.168	0.8662	
2008 - 2002 == 0	6.2748	23.5072	0.267	0.7895	
2010 - 2002 == 0	12.5137	24.4153	0.513	0.6083	
2011 - 2002 == 0	17.4794	24.8029	0.705	0.4810	
2012 - 2002 == 0	16.4959	24.7068	0.668	0.5043	
2013 - 2002 == 0	22.7604	24.7255	0.921	0.3573	
2014 - 2002 == 0	35.0505	28.6460	1.224	0.2211	
2015 - 2002 == 0	48.5936	30.0244	1.618	0.1056	
2004 - 2003 == 0	5.8857	20.3814	0.289	0.7728	
2005 - 2003 == 0	7.1364	20.3372	0.351	0.7257	
2006 - 2003 == 0	10.8505	20.5012	0.529	0.5966	
2007 - 2003 == 0	17.3211	21.1206	0.820	0.4122	
2008 - 2003 == 0	19.6398	21.1953	0.927	0.3541	
2010 - 2003 == 0	25.8787	22.1816	1.167	0.2433	
2011 - 2003 == 0	30.8444	22.6016	1.365	0.1723	
2012 - 2003 == 0	29.8609	22.5414	1.325	0.1853	
2013 - 2003 == 0	36.1254	22.5792	1.600	0.1096	
2014 - 2003 == 0	48.4155	26.8335	1.804	0.0712	.
2015 - 2003 == 0	61.9586	28.3194	2.188	0.0287	*
2005 - 2004 == 0	1.2507	19.9729	0.063	0.9501	
2006 - 2004 == 0	4.9648	20.1938	0.246	0.8058	
2007 - 2004 == 0	11.4354	20.7954	0.550	0.5824	
2008 - 2004 == 0	13.7541	20.9244	0.657	0.5110	
2010 - 2004 == 0	19.9930	21.9883	0.909	0.3632	
2011 - 2004 == 0	24.9586	22.4139	1.114	0.2655	
2012 - 2004 == 0	23.9752	22.3402	1.073	0.2832	
2013 - 2004 == 0	30.2397	22.3419	1.353	0.1759	
2014 - 2004 == 0	42.5298	26.6091	1.598	0.1100	
2015 - 2004 == 0	56.0728	28.0772	1.997	0.0458	*
2006 - 2005 == 0	3.7141	19.7503	0.188	0.8508	
2007 - 2005 == 0	10.1847	20.4009	0.499	0.6176	
2008 - 2005 == 0	12.5034	20.4844	0.610	0.5416	
2010 - 2005 == 0	18.7423	21.5600	0.869	0.3847	
2011 - 2005 == 0	23.7080	22.0028	1.077	0.2813	
2012 - 2005 == 0	22.7245	21.9997	1.033	0.3016	
2013 - 2005 == 0	28.9890	21.9734	1.319	0.1871	
2014 - 2005 == 0	41.2791	26.2763	1.571	0.1162	
2015 - 2005 == 0	54.8222	27.7519	1.975	0.0482	*
2007 - 2006 == 0	6.4706	20.4162	0.317	0.7513	
2008 - 2006 == 0	8.7893	20.4813	0.429	0.6678	
2010 - 2006 == 0	15.0282	21.5043	0.699	0.4846	
2011 - 2006 == 0	19.9939	21.9714	0.910	0.3628	
2012 - 2006 == 0	19.0104	21.9986	0.864	0.3875	
2013 - 2006 == 0	25.2749	22.0313	1.147	0.2513	

2014 - 2006 == 0	37.5650	26.3395	1.426	0.1538
2015 - 2006 == 0	51.1081	27.8242	1.837	0.0662 .
2008 - 2007 == 0	2.3187	21.0432	0.110	0.9123
2010 - 2007 == 0	8.5576	22.0702	0.388	0.6982
2011 - 2007 == 0	13.5232	22.5161	0.601	0.5481
2012 - 2007 == 0	12.5398	22.5303	0.557	0.5778
2013 - 2007 == 0	18.8043	22.5784	0.833	0.4049
2014 - 2007 == 0	31.0944	26.7849	1.161	0.2457
2015 - 2007 == 0	44.6375	28.2647	1.579	0.1143
2010 - 2008 == 0	6.2389	21.9513	0.284	0.7762
2011 - 2008 == 0	11.2046	22.3986	0.500	0.6169
2012 - 2008 == 0	10.2211	22.4813	0.455	0.6494
2013 - 2008 == 0	16.4856	22.4436	0.735	0.4626
2014 - 2008 == 0	28.7757	26.7162	1.077	0.2814
2015 - 2008 == 0	42.3188	28.1293	1.504	0.1325
2011 - 2010 == 0	4.9656	23.1956	0.214	0.8305
2012 - 2010 == 0	3.9822	23.3042	0.171	0.8643
2013 - 2010 == 0	10.2467	23.3472	0.439	0.6607
2014 - 2010 == 0	22.5368	27.4534	0.821	0.4117
2015 - 2010 == 0	36.0798	28.9333	1.247	0.2124
2012 - 2011 == 0	-0.9834	23.6609	-0.042	0.9668
2013 - 2011 == 0	5.2811	23.7216	0.223	0.8238
2014 - 2011 == 0	17.5711	27.8200	0.632	0.5276
2015 - 2011 == 0	31.1142	29.2609	1.063	0.2876
2013 - 2012 == 0	6.2645	23.7040	0.264	0.7916
2014 - 2012 == 0	18.5545	27.7948	0.668	0.5044
2015 - 2012 == 0	32.0976	29.2460	1.098	0.2724
2014 - 2013 == 0	12.2901	27.7371	0.443	0.6577
2015 - 2013 == 0	25.8332	29.1041	0.888	0.3747
2015 - 2014 == 0	13.5431	32.2955	0.419	0.6750

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Adjusted p values reported -- none method)

Appendix 11

Xestospongia muta lme and *Tukey's post-hoc* analysis

```
Linear mixed-effects model fit by REML
 Data: xest
      AIC     BIC    logLik
  11333.65 11351.9 -5662.825

Random effects:
 Formula: ~1 | LOCATION
        (Intercept) Residual
StdDev:    388.9544 690.8835

Fixed effects: AREA ~ YEAR
               Value Std.Error   DF   t-value   p-value
(Intercept) -82394.37 11963.140  686 -6.887353   0
YEAR            41.37     5.963  686  6.936739   0
 Correlation:
     (Intr)
YEAR -1

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-2.8076442 -0.5183953 -0.1747198  0.3284804  4.8491843
Number of Observations: 710
Number of Groups: 23
Simultaneous Tests for General Linear Hypotheses
Multiple Comparisons of Means: Tukey Contrasts
Fit: lme.formula(fixed = AREA ~ YEAR, data = xest, random = list(~1 |
    LOCATION))

Linear Hypotheses:
                 Estimate Std. Error z value Pr(>|z|)
2001 - 2000 == 0   17.355    152.674   0.114 0.909496
2002 - 2000 == 0  -46.586    161.683  -0.288 0.773244
2003 - 2000 == 0  -57.190    162.331  -0.352 0.724609
2004 - 2000 == 0  -83.000    157.231  -0.528 0.597577
2005 - 2000 == 0  -47.948    157.595  -0.304 0.760940
2006 - 2000 == 0   30.922    157.273   0.197 0.844131
2007 - 2000 == 0   91.626    160.950   0.569 0.569164
2008 - 2000 == 0  149.126    156.641   0.952 0.341084
2010 - 2000 == 0  288.997    157.502   1.835 0.066523 .
2011 - 2000 == 0  329.956    155.771   2.118 0.034157 *
2012 - 2000 == 0  299.293    157.145   1.905 0.056836 .
2013 - 2000 == 0  384.790    153.578   2.506 0.012228 *
2014 - 2000 == 0  446.797    157.324   2.840 0.004512 **
2015 - 2000 == 0  498.461    158.563   3.144 0.001669 **
2002 - 2001 == 0  -63.942    160.508  -0.398 0.690357
2003 - 2001 == 0  -74.545    161.060  -0.463 0.643478
2004 - 2001 == 0 -100.355    155.946  -0.644 0.519883
2005 - 2001 == 0  -65.303    156.303  -0.418 0.676098
2006 - 2001 == 0   13.567    155.972   0.087 0.930686
2007 - 2001 == 0   74.271    159.664   0.465 0.641810
```

2008 - 2001 == 0	131.771	155.337	0.848	0.396276	
2010 - 2001 == 0	271.642	156.197	1.739	0.082018	.
2011 - 2001 == 0	312.601	154.458	2.024	0.042984	*
2012 - 2001 == 0	281.938	155.836	1.809	0.070421	.
2013 - 2001 == 0	367.435	152.255	2.413	0.015809	*
2014 - 2001 == 0	429.442	156.013	2.753	0.005913	**
2015 - 2001 == 0	481.106	157.257	3.059	0.002218	**
2003 - 2002 == 0	-10.604	152.791	-0.069	0.944670	
2004 - 2002 == 0	-36.414	148.133	-0.246	0.805822	
2005 - 2002 == 0	-1.361	148.314	-0.009	0.992678	
2006 - 2002 == 0	77.508	147.591	0.525	0.599474	
2007 - 2002 == 0	138.212	151.353	0.913	0.361149	
2008 - 2002 == 0	195.713	147.068	1.331	0.183267	
2010 - 2002 == 0	335.583	147.771	2.271	0.023149	*
2011 - 2002 == 0	376.543	146.023	2.579	0.009919	**
2012 - 2002 == 0	345.879	147.445	2.346	0.018985	*
2013 - 2002 == 0	431.377	143.784	3.000	0.002698	**
2014 - 2002 == 0	493.383	147.500	3.345	0.000823	***
2015 - 2002 == 0	545.048	148.771	3.664	0.000249	***
2004 - 2003 == 0	-25.810	146.955	-0.176	0.860583	
2005 - 2003 == 0	9.243	147.107	0.063	0.949901	
2006 - 2003 == 0	88.112	146.326	0.602	0.547065	
2007 - 2003 == 0	148.816	150.090	0.992	0.321435	
2008 - 2003 == 0	206.316	145.760	1.415	0.156934	
2010 - 2003 == 0	346.187	146.434	2.364	0.018073	*
2011 - 2003 == 0	387.147	144.642	2.677	0.007438	**
2012 - 2003 == 0	356.483	146.099	2.440	0.014687	*
2013 - 2003 == 0	441.981	142.349	3.105	0.001903	**
2014 - 2003 == 0	503.987	146.065	3.450	0.000560	***
2015 - 2003 == 0	555.651	147.299	3.772	0.000162	***
2005 - 2004 == 0	35.053	141.898	0.247	0.804887	
2006 - 2004 == 0	113.922	141.322	0.806	0.420175	
2007 - 2004 == 0	174.626	145.286	1.202	0.229383	
2008 - 2004 == 0	232.126	140.683	1.650	0.098943	.
2010 - 2004 == 0	371.997	141.348	2.632	0.008494	**
2011 - 2004 == 0	412.957	139.412	2.962	0.003055	**
2012 - 2004 == 0	382.293	140.842	2.714	0.006641	**
2013 - 2004 == 0	467.791	137.100	3.412	0.000645	***
2014 - 2004 == 0	529.797	140.916	3.760	0.000170	***
2015 - 2004 == 0	581.461	142.232	4.088	4.35e-05	***
2006 - 2005 == 0	78.869	141.244	0.558	0.576576	
2007 - 2005 == 0	139.574	145.106	0.962	0.336114	
2008 - 2005 == 0	197.074	140.586	1.402	0.160974	
2010 - 2005 == 0	336.944	141.221	2.386	0.017036	*
2011 - 2005 == 0	377.904	139.270	2.713	0.006658	**
2012 - 2005 == 0	347.240	140.712	2.468	0.013597	*
2013 - 2005 == 0	432.738	136.961	3.160	0.001580	**
2014 - 2005 == 0	494.744	140.714	3.516	0.000438	***
2015 - 2005 == 0	546.409	142.099	3.845	0.000120	***
2007 - 2006 == 0	60.704	144.348	0.421	0.674090	
2008 - 2006 == 0	118.204	139.626	0.847	0.397229	
2010 - 2006 == 0	258.075	140.363	1.839	0.065970	.
2011 - 2006 == 0	299.034	138.392	2.161	0.030713	*
2012 - 2006 == 0	268.371	139.851	1.919	0.054987	.

```
2013 - 2006 == 0  353.869    136.007   2.602 0.009272 **
2014 - 2006 == 0  415.875    139.938   2.972 0.002960 **
2015 - 2006 == 0  467.539    141.238   3.310 0.000932 ***
2008 - 2007 == 0   57.500    143.679   0.400 0.689009
2010 - 2007 == 0  197.371    144.375   1.367 0.171602
2011 - 2007 == 0  238.330    142.481   1.673 0.094382 .
2012 - 2007 == 0  207.667    143.947   1.443 0.149117
2013 - 2007 == 0  293.164    140.208   2.091 0.036535 *
2014 - 2007 == 0  355.171    143.922   2.468 0.013594 *
2015 - 2007 == 0  406.835    145.267   2.801 0.005101 **
2010 - 2008 == 0  139.871    139.661   1.002 0.316583
2011 - 2008 == 0  180.830    137.645   1.314 0.188932
2012 - 2008 == 0  150.167    139.111   1.079 0.280376
2013 - 2008 == 0  235.664    135.241   1.743 0.081412 .
2014 - 2008 == 0  297.671    139.210   2.138 0.032493 *
2015 - 2008 == 0  349.335    140.524   2.486 0.012921 *
2011 - 2010 == 0   40.959    138.284   0.296 0.767079
2012 - 2010 == 0   10.296    139.714   0.074 0.941254
2013 - 2010 == 0   95.794    135.920   0.705 0.480948
2014 - 2010 == 0  157.800    139.731   1.129 0.258765
2015 - 2010 == 0  209.464    141.094   1.485 0.137656
2012 - 2011 == 0  -30.663    137.626  -0.223 0.823689
2013 - 2011 == 0   54.834    133.803   0.410 0.681943
2014 - 2011 == 0  116.840    137.666   0.849 0.396035
2015 - 2011 == 0  168.505    139.059   1.212 0.225607
2013 - 2012 == 0   85.498    135.306   0.632 0.527465
2014 - 2012 == 0  147.504    139.113   1.060 0.289000
2015 - 2012 == 0  199.168    140.467   1.418 0.156221
2014 - 2013 == 0   62.006    135.230   0.459 0.646575
2015 - 2013 == 0  113.671    136.659   0.832 0.405530
2015 - 2014 == 0   51.664    140.389   0.368 0.712867
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Adjusted p values reported -- none method)
```